Firestorms in a mesic savanna-forest mosaic

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Abstract

Forests and savannas in a savanna-forest mosaic are maintained by positive feedback loops with fires, promoting fires in savannas and excluding fires in forests. Occasional extreme fires do however burn into forest edges and cause extensive mortality. So, while our understanding of bistability in these systems has advanced, our understanding of biome-level change has remained rather static. Very few studies address the issue of forest to savanna transitions following extreme fire events. This study is posed to address the criticisms surrounding the bistability of savanna and forest vegetation and present evidence for catastrophic regime shifts in these mosaic systems. What sets it apart from previous research is the boundary between vegetation types is naturally occurring, not the result of logging within forests and the subsequent damage by fire. In HiP, forest patches naturally abut savannas, the system has its native herbivores, and human impacts are low.

In my thesis I explored the circumstances causing a catastrophic regime shift or recovery of a resilient forest boundary. I initially set out to determine the drivers of vegetation distributions and dynamics in Hluhluwe-iMfolozi Park (HiP). Next I documented the aftermath of an extreme fire in thicket, forest and savanna vegetation focusing on the recovery of vegetation and evidence for catastrophic regime shifts. And lastly, I explored the association between bark thickness and commonly measured traits in order to understand trait evolution in response to fire regime and other selective pressures such as herbivory and drought.

Using aerial photographs from six time periods between 1937 and 2013, I mapped vegetation changes in Hluhluwe iMfolozi Park. Using a Generalized Additive Model (GAM) I built a Habitat Suitability Index (HSI) map based on vegetation distribution maps and topographic variables related to fire behaviour. I investigated transitions between time periods based on the HSI map, as well as the effects of neighbourhood on transition probabilities. Forest distributions in HiP have not remained static over time and have expanded into areas that were once savannas. The habitat suitability index, using topographic predictors associated with fire behaviour, relates to the expansion and contraction of forest vegetation. The expansion and contraction dynamics are however more nuanced, with the in situ vegetation neighbourhood playing a large role. This is a dynamic system where both forest and savanna boundaries can and have changed considerably.

The mechanism proposed here allowing for forest establishment is a local scale modification of fire regime creating pockets where fires are most likely to peter out resulting in patches with low fire return intervals. Fire sensitive vegetation establishes and persists in areas where the fire return interval is lower due to a topographic hindrance on fire spread. As opposed to widely available correlative approaches, a mechanistic understanding of fire spread and behaviour on complex terrain could advance our understanding of savanna-forest co-existence and provide insight into the presence and persistence of enigmatic forest patches in a fire-prone ecosystem.

I used a fire spread model to predict fire behaviour (rate of spread) based on different wind directions and speeds in Hluhluwe Game Reserve on a homogeneous fuel layer to focus explicitly on the interaction between fire, topography and wind. Fire behaviour predictions were then compared to the earliest records of forest distributions, captured in aerial photographs in 1937. Wind direction used in the prediction of fire behaviour had a significant effect on the distribution of 'fire shadows'. Large portions of the landscape show lower rates of spread. When predictions are based on actual fire season conditions these areas are generally occupied by forests.

Fire refugia are important for the long term persistence of forests in fire prone landscapes. The firestorms in HiP crossed the boundary from savannas to closed woody vegetation with ease, switching from highly flammable grass fuels to forest leaf litter, understorey shrubs and herbs, and woody biomass, causing widespread mortality and topkill of adult trees. Extreme fires provide the opportunity for a biome switch from forest and thicket systems to savanna systems, even within these refugia. However, the timing of subsequent fires is vital for the colonisation and establishment of flammable grass clades and a savanna fire regime. Fire suppression within these mosaics may lead to a loss of resilience of forest margins as the seed bank of these pioneer species is depleted over time. In the future, chance fires which are not suppressed will lead to larger losses of forest area as shade intolerant pioneer species are not readily available to reclaim forest edges.

There are clear differences in the drivers between high biomass forests and low biomass savannas, despite relatively similar net primary productivity. Much of the earlier trait based literature was assembled in temperate deciduous forests. If forests and savannas are ASS, they should persist long enough for discrete traits to diverge in the two systems with

contrasting fire responses at the centre of these trait differences. Disturbance regime, as opposed to climate, is gaining recognition as a global driver of ecosystem functioning. The plant functional traits (PFT) governing fitness of forest and savanna trees differ. Within savanna trees, PFTs differ between demographic stages and the disturbance regime (type, history, severity, intensity of disturbance). Disturbance prone trees have developed a number of strategies, including clonal spread and belowground bud banks allowing basal resprouting. The difficulty going forward is to assimilate these traits into existing global frameworks. We explored the association between bark thickness and commonly measured traits in order to understand trait evolution in response to fire regime and other selective pressures such as herbivory and drought. Forest margins appear to be far more resilient, where they occur in mosaics with savannas in Africa, than forest interiors in the neotropics.

Understanding the nature and extent of these impacts in African savannas is crucial due to the direct dependence of a large marginalized, vulnerable, rural population on savanna ecosystem services for agriculture and grazing. As climate changes, there is the potential for surprises such as more firestorms, as fire regimes are closely coupled to climate. An increase in these extreme events would allow more opportunities for catastrophic regime shifts and losses of forest vegetation. How does one reconcile lengthening fire seasons and more extreme fires with an increase in woody biomass? And what predictions can we make for the future of African savannas and forests?

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First and foremost, I would like to acknowledge my mentor William Bond. From my first research project with you in 2010, to watching thunderstorms develop while drinking gin on a hotel rooftop in Brazil, to the baptism of fire you orchestrated with conference presentations which helped me get over my crippling fear of public speaking, to herding professors on a cross country workshop as a stand in 'William Blonde' (thanks to Matt Trisos) who apparently knows all about South Africa's geological landforms and is an expert at species identification, to bedside chats about Terry Pratchett in the ICU and your endless pursuit of pudding – you have moulded my thinking, directed/reigned in my tangents and helped me navigate the 'oceans of white space'. Over the last decade you have had more influence in all spheres of my life than anyone else, and I cannot thank you enough for guiding me to where I am today.

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I started my PhD at the tail end of Williams's tenure at UCT, so I did not have a large supportive lab group or many ecology minded people to bounce ideas off. Two people who really stand out for me are Nikki Stevens and Tristan Charles-Dominique. Nikki has gone out of her way to force me into being her friend (or more accurately, to realise how lucky I am to count her as a friend), and helped me navigate the somewhat convoluted world of academia and conference etiquette. Tristan, who encouraged my creativity, taught me how to deal with critics, and taught me more about botany in the field than I picked up in three years of undergraduate courses. My sincerest thanks to the both of you, I look forward to many adventures in the future. To the special friends in my life, those who know what I'm doing (Julia van Velden, Oliver Cowan, Matthew Trisos), and those who just like telling people I burn

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Lastly, to Mum, Dad, and Megs. From running around gathering seeds during picnic stops on trips to game reserves, to playing hide and seek in our favourite nurseries, being taught to question everything, the three of you have always inspired and supported me. From housing stranded researchers and logistical support during fieldwork to housing me for the last couple months while I have been writing this thesis, you have been selfless, generous and have imbued within me the energy to finish at last! This is for the three of you, I love you always.

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Abbreviations Used

ASS – *Alternative Stable States*

ASTER – *Advanced Spaceborne Thermal Emission and Reflection Radiometer*

DEM – *Digital Elevation Model*

DGVM – *Dynamic Global Vegetation Model*

DPM – *Disk Pasture Meter*

EKZNW – *Ezemvelo KwaZulu Natal Wildlife*

FF – *Fire Frequency*

GAM – *Generalized Additive Model*

GDEM – *Global Digital Elevation Model*

GLM – *Generalized Linear Model*

HiP – *Hluhluwe iMfolozi Park*

HGR – *Hluhluwe Game Reserve*

HSI – *Habitat Suitability Index*

iGR – *iMfolozi Game Reserve*

LMA – *Leaf Mass Area*

MAP – *Mean Annual Precipitation*

MAT – *Mean Annual Temperature*

MODIS – *Moderate Resolution Imaging Spectroradiometer*

NMDS – *Non-metric Multidimensional Scaling*

NPP – *Net Primary Productivity*

PCA – *Principle Component Analysis*

PFT – *Plant Functional Trait*

QDS – *Quarter Degree Square*

ROS – *Rate of Spread*

SLA – *Specific Leaf Area*

TC – *Tree Cover*

TRMM – *Tropical Rainfall Measuring Mission*

VCF – *Vegetation Continuous Fields*

WD - *Wood Density*

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Chapter 1

Introduction

1.1. General Introduction

Understanding the drivers and determinants of biome boundaries and their role in driving change in biomes is critical for predicting biome responses to global change (Hoffman *et al*, 2003; Midgley *et al*, 2010; Tilman, 1990). Among the least understood of these drivers is fire, which influences the structure and distribution of biomes globally (Bond, 2008; Bond et al, 2005; Staver et al, 2012). At a landscape scale, interactions between fire and vegetation often result in a vegetation mosaic of fire-adapted (e.g. savannas and fynbos) and fire-sensitive (e.g. forests) vegetation communities (Hoffmann et al, 2009). The savanna-forest-thicket mosaic in north eastern South Africa is a prime example of this. The boundary between these biomes is abrupt, resulting in a complete shift in tree density and species composition over the scale of meters. Ecological and physiological differences between these suites of species play a dominant role in vegetation responses to fire at both an individual and biome level and hence the location of the biome boundary (Hoffmann et al, 2012a).

The biomes in these mosaics are recognised as alternative stable states, such that a given set of environmental conditions can support either biome in a stable, non-transitory state (Scheffer and Carpenter, 2003; Hirota et al, 2011). Savannas are characterized by a tree-grass matrix that is very flammable and burns every 1-3 years (Hoffman *et al*, 2009, Sankaran *et al*, 2005), while forests and thickets exclude fires via fuel limitations and microclimate amelioration (Hoffmann et al, 2012b). However occasional fires do penetrate forests and cause extensive mortality (Cochrane, 2003). The role of these occasional fires – known as “firestorms/megafires” – in eroding the bistability of savanna and forest over long or even medium time scales is poorly understood, but is increasingly relevant in the context of climatic change. Moreover, response of forests to these fires is largely unknown, making an understanding of fire as a driver of biome-level change (rather that biome bistability) impossible.

My thesis aims to address the issue of fire as a driver of change at savanna-forest and savanna-thicket boundaries, making use of savanna-forest-thicket mosaics and recent invasions of forest by savanna fires in Hluhluwe iMfolozi Park, South Africa.

1.2. Alternative Stable States

The Alternative Stable States hypothesis, first proposed in the 1960's (Lewontin, 1969; Holling, 1973; May, 1977), has played a large role in shaping how ecologists view ecosystems, and more importantly, the stability of ecosystems over time (Scheffer et al, 2001; Scheffer and Carpenter, 2003). Scheffer et al (2001) outline three responses of dynamic ecosystems to changing conditions; (1) a smooth response where the ecosystem state changes gradually as conditions change, (2) a rapid transition from one ecosystem state to another once conditions reach a critical threshold and (3) a non-linear or discontinuous response. In the latter case, under a certain range of conditions, two stable and one unstable equilibria exist (Figure 1.1); hence two stable ecosystem states can occupy the same area.

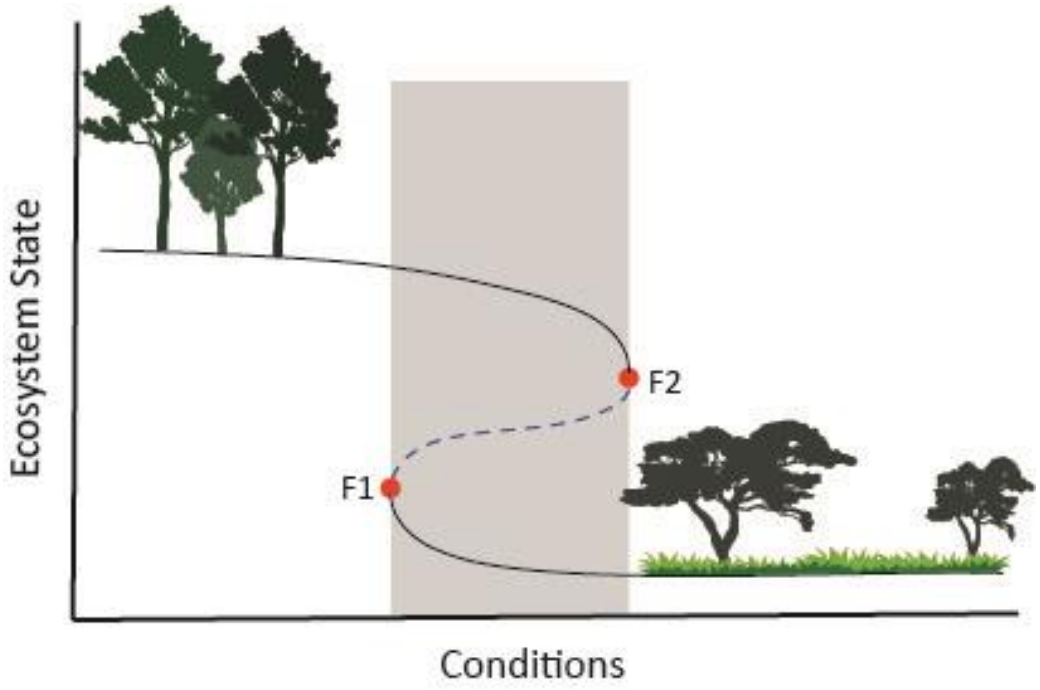
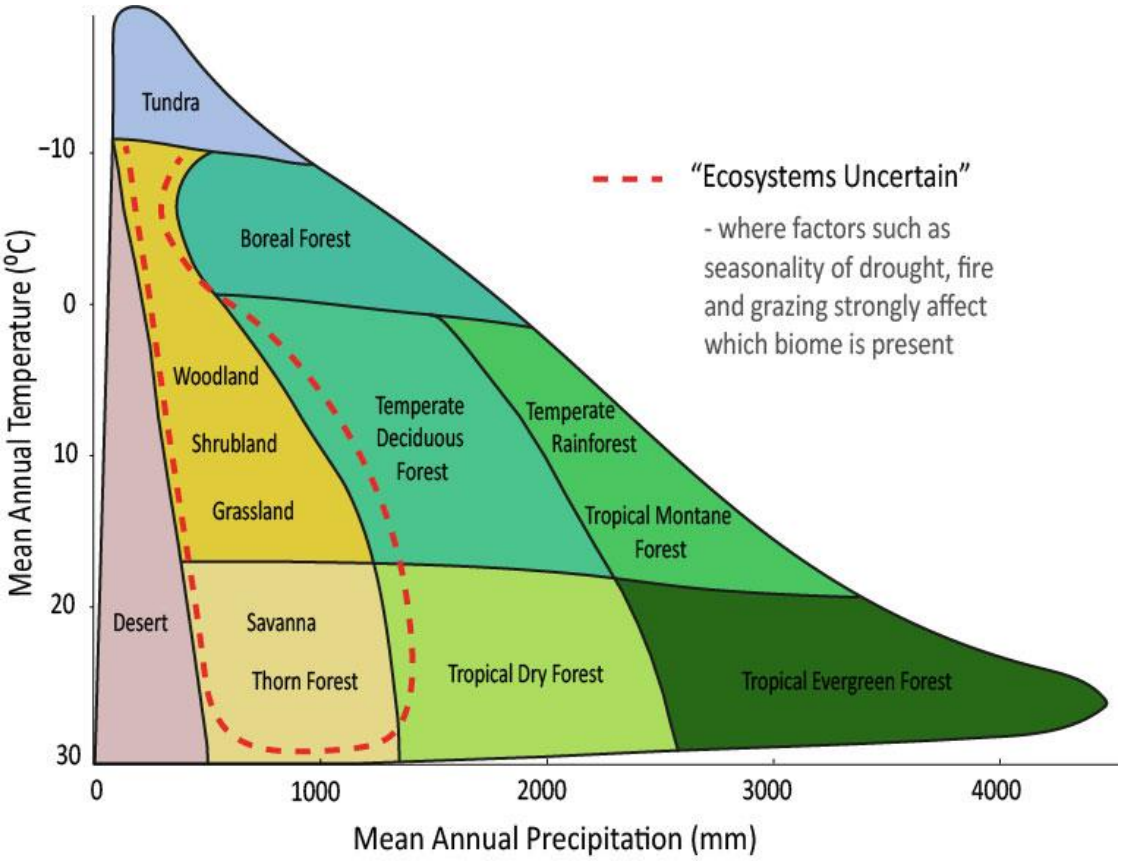


Figure 1.1. Schematic of a discontinuous ecosystem response to changing environmental conditions. Shaded area represents the range of conditions where both ecosystems are supported. Modified from Scheffer and Carpenter (2003).

The equilibrium into which the system settles is determined by its initial state, a process known as path dependency (Scheffer et al, 2001; Levin, 1998). As conditions change, the ecosystem reaches a bifurcation point (F_2) where a 'catastrophic transition' occurs and the ecosystem settles into a new equilibrium or alternative stable state (Scheffer and Carpenter, 2003). In order to transition back to the original ecosystem state, conditions need to return

to a point (F_1) lower than the initial bifurcation point (Figure 1.1). Many early examples of alternative stable states were highly criticized (Connell and Sousa, 1983), however more recent examples show evidence of alternative stable states in a diverse array of ecosystems (see Schroder et al, 2005) but the topic is still controversial and debated (Petraitis, 2013). This thesis will focus on alternative stable states in vegetation communities.

Traditionally global vegetation distribution is considered to be, in most parts, closely coupled to climatic conditions (Holdridge, 1947; Whittaker, 1975; Henderson-Sellers, 1994). This observation led to the development of a number of classification schemes (most notably Holdridge, 1947 and Whittaker, 1975) which employ a bioclimatic envelope approach to predict global vegetation distributions (Henderson-Sellers, 1994). Whittaker (1975) outlines the difficulties in applying this approach and recognises a range of conditions for which this relationship does not hold (Figure 1.2).



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Within this 'uncertain ecosystems' envelope there is the potential for a system to support grasslands, shrublands, woodlands or forests (Whittaker, 1975; Bond, 2005). Climatic factors, essentially, set the limit for potential plant growth; however the realized vegetation is a result of the complex interactions of a suite of biotic and abiotic drivers (Bond, 2005). Despite the narrow range of conditions encompassed by the 'uncertain ecosystem' envelope, it accounts for a substantial portion of the earth's terrestrial surface (Fig. 1. in Bond 2005). Of particular interest to this thesis is the savanna-forest mosaic where the climatic vegetation potential is not reached (Figure 1.3) due to the complex interactions of a number of drivers, most notably soil properties, fire and herbivory (Whittaker, 1975; Bond, 2005; Sankaran et al, 2005).

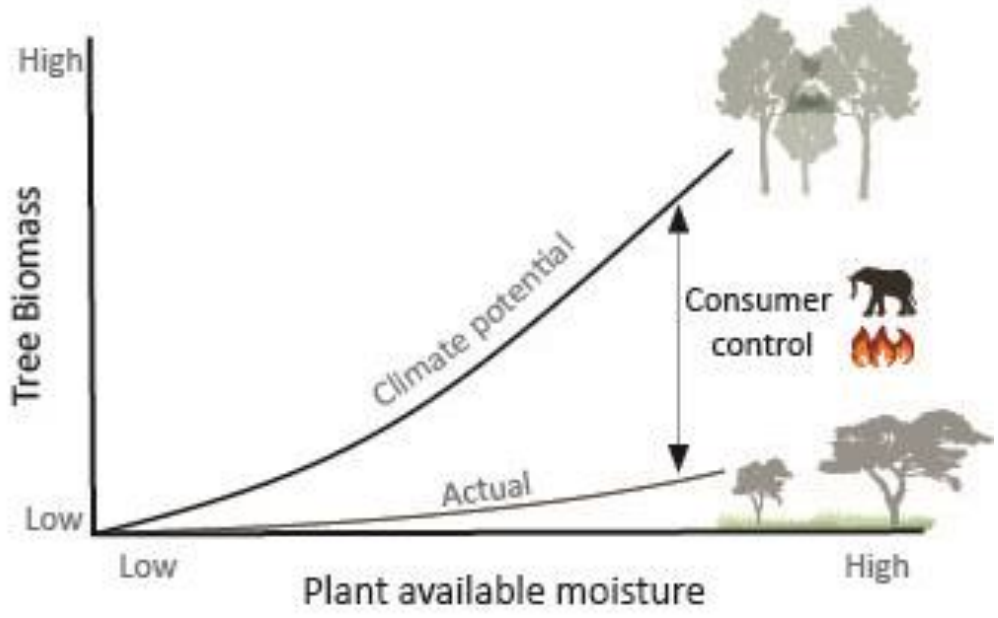


Figure 1.3. Assessing consumer control of tree biomass. The extent of consumer control of an ecosystem can be measured as the difference between tree biomass at 'climate potential' and the actual tree biomass. Modified from Bond and Keeley (2005).

The savanna biome is a dynamic biome defined by the presence of a continuous C4 grass layer interspersed with trees (Sankaran *et al*, 2005; Scholes and Archer, 1997). Sankaran *et al*. (2005, 2008) found that woody cover is largely limited by mean annual precipitation until a threshold of 650mm, above which disturbances and other regulatory variables are the main limitation to woody cover. These regulatory variables fall into two broad categories: "top-down" and "bottom-up" controls (Staver *et al*, 2009; Weltzin and Coughenour, 1990). Bottom-up controls encompass resource-limiting factors such as water availability, soil

nutrients, and access to light (Weltzin and Coughenour, 1990), while top-down controls describe disturbance regimes such as fire and herbivory (Bond, 2008).

Figure 1.4. Sharp boundaries between (left) thicket and savanna vegetation, and (right) forest and savanna vegetation in Hluhluwe iMfolozi Park. Photos taken by Heath Beckett

It is clear that while low rainfall limits maximum woody cover, rainfall alone fails to explain what limits woody plants in wetter regions that should support closed canopy forest. This issue is highlighted in regions where open grasslands and savannas occur in the presence of dense forests, creating landscape mosaics with abrupt boundaries (see Figure 1.4) between vegetation types (Warman and Moles, 2009). Examples of these vegetation mosaics are found in Brazil (Hoffmann et al, 2009), Ghana (Markham and Babbedge, 1979; Swaine, 1992), the Central African Republic (Beauvais, 2009), Gabon (Jeffery *et al*, 2014), Ivory Coast (Goetze et al, 2006; Hennenberg et al, 2006), India (Mariotti and Peterschmitt, 1994; Puyravaud et al, 1994), Madagascar (Virah-Sawmy, 2009), New Caledonia (Perry and Enright, 2002; Stevenson and Hope, 2005) and Australia (Bowman, 2009).

1.3. Savanna-Forest Dynamics

Recently, on a global scale, Lehmann *et al* (2011) presented a range of environmental conditions in which savannas occur; however they also state that "some proportion of the land is always not-savanna". Staver *et al* (2011) demonstrated that tree cover is limited by the amount and the seasonality of rainfall; they also highlighted the critical role of fire in the differentiation of high and low tree cover (i.e. forest and savanna, respectively) in areas receiving intermediate rainfall (from 1000 mm to 2500 mm per year). Fire limits woody cover by preventing tree recruitment, as saplings are continually stuck in what has been termed the "fire-trap" until they are afforded the opportunity to escape by growing into adult trees (Bell, 1984; Higgins *et al*, 2000; Bond and Midgley, 2001). It is widely accepted that positive feedback loops with fire maintain forest and savanna patches in these mosaics (Wilson and Agnew, 1992; Geiger *et al*, 2011). Experimental exclusion of fires in mesic savannas is usually followed by an increase in woody biomass and forest species which is used as evidence for alternative stable states (Warman and Moles, 2009; Hoffmann *et al*, 2012; Murphy and Bowman, 2012).

Despite a growing acceptance of the idea that savannas and forests represent alternative stable states, there is strong criticism surrounding the methods used and interpretation of data (Veenendaal *et al*, 2014; Hanan *et al*, 2013). An alternative, and older hypothesis, is that different vegetation communities occur on different soils. The implication is that though the climate may be suitable for forest edaphic constraints prevent the formation of forests. In Australia, for example, soil phosphorus has long been thought to determine the boundary between 'rainforests' (closed forest) and sclerophyll (eucalypt-dominated) open woodlands (Beadle, 1958). Modern proponents of edaphic control of major vegetation patterns include Veenendaal *et al* (2015), Lloyd *et* al (2015) and Mills *et al* (2013). See Lloyd and Veenendaal (2016) for a strongly worded rebuke of fire-mediated alternative stable states in savannas and forests.

Edaphic control implies that forest/savanna distribution will be very stable. ASS theory also argues for stability but includes the possibility of 'regime shifts'. These are sudden shifts from one state to another. The destruction of forest by a large fire, and its replacement by a

savanna would be an example of a regime shift. However, such shifts may be very rarely observed. The reverse, from a savanna to a forest, would not be predicted by the edaphic constraints hypothesis but is predicted by ASS. However instead of being abrupt, the process consists of a gradual change in ecosystem properties with an eventual tipping point where forest elements exclude fire, savanna grassy layers are shaded out, and the system switches to a forest. Regime shifts are the subject of this thesis, both directions are covered.

Very few studies address the issue of forest to savanna transitions following extreme fire events. This study is posed to address the criticisms surrounding the bistability of savanna and forest vegetation and present evidence for catastrophic regime shifts in these mosaic systems. What sets it apart from previous research is the boundary between vegetation types is naturally occurring, not the result of logging within forests and the subsequent damage by fire.

"...The boundaries of communities have received little critical study; they have been considered by many as lacking in interest and unworthy of investigation (vide Lippmaa, 1933a:13). The possibility that different degrees of discontinuity between associations exist was indicated by Du Rietz (1923a, 1923b); as there are "good" and "weak" species, so there may be "good" associations with sharp boundaries and "weak" associations with more gradual transitions and arbitrary boundaries."

- Whittaker (1962)

1.4. Thesis structure and aims

The body of this thesis consists of four chapters written as stand-alone research papers. The intention is to submit these chapters for publication after the examination process. All references are compiled in one bibliography at the end of the dissertation. The introductory chapter provides a detailed overview of the topic and an account of notable previous research. The study site chapter highlights the diversity present in Hluhluwe iMfolozi Park and recently published research specific to the biotic and abiotic template of the park. The synthesis distils the key findings from all chapters, and discusses how these findings relate to the initial aims of the thesis and the contributions made to the field. I will briefly explain the questions and hypotheses of each chapter below, and how these contribute to the overall aim of the thesis.

In my thesis I wished to explore the circumstances causing a catastrophic regime shift or recovery of a resilient forest boundary. To this end, I initially set out to determine the drivers of vegetation distributions and dynamics in **Chapters 3** and **4.**

Chapter 3: Here I attempt to answer whether or not complex topography facilitates the establishment and persistence of fire sensitive (forest) vegetation in a fire prone landscape. Forest distributions in HiP have not remained static over time and have expanded into areas that were once savannas. This is a dynamic system where both forest and savanna boundaries can change considerably. Fire refugia are important for the long term persistence of forests in fire prone landscapes. Fire sensitive vegetation establishes and persists in areas where the fire return interval is lower due to a topographic hindrance on fire spread.

Chapter 4: Following on from the results of Chapter 3, I tested the idea that fire is the major determinant of vegetation distribution. I based this on the relationship between simulated fire behaviour and the distribution of closed canopy vegetation in the oldest aerial photograph imagery available to capture patterns least impacted by land use changes, road development and settlements. When using average weather conditions for the fire season, simulated fire behaviour across the complex terrain of HiP was a good predictor of historical vegetation distributions. The model also allowed me to investigate scenarios where extreme fires are the norm, using fire weather conditions matching that of the firestorms events which precipitated this thesis.

My second objective was to document the aftermath of an extreme fire in thicket, forest and savanna vegetation in **Chapter 5**, focusing on the recovery of vegetation and catastrophic regime switches. The events that led to this study, firestorms, are rare extreme events. They crossed the boundary from savannas to closed woody vegetation with ease, switching from highly flammable grass fuels to forest leaf litter, understorey shrubs and herbs, and woody biomass, effectively opening up the environment through the widespread mortality and topkill of adult trees. How, if at all, does a fire averse vegetation type, such as forest or thicket, recover from this? I was not able to set up long term monitoring plots and logging equipment (HiP is a natural park with a full suite of African animals, some of which have a particular fondness for destroying expensive equipment), instead I used repeat transects and space-for-time substitutions to monitor the effects of these catastrophic events on vegetation communities over time.

Lastly, there are clear differences in the drivers between high biomass forests and low biomass savannas, despite relatively similar net primary productivity. In the last few years the functional trait literature on disturbance-prone ecosystems has taken off (Clarke *et* al, 2013; Fidelis *et al*, 2014; Pausas *et al,* 2018), with a wider acceptance of the role of disturbance regime, as opposed to climate, determining the distribution of savanna trees (Stevens *et al*, 2018). If forests and savannas are ASS, they should persist long enough for discrete traits to diverge in the two systems with contrasting fire responses at the center of these trait differences. In **Chapter 6** we explored the association between bark thickness and commonly measured traits in order to understand trait evolution in response to fire regime and other selective pressures such as herbivory and drought.

Preface: Chapter 2

This chapter outlines the study site where the majority of the fieldwork was conducted: Hluhluwe iMfolozi Park. Sections 2.2 and 2.3 are modified versions of my contributions to a book, *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*, published by Cambridge University Press in 2017. Section 2.2 includes my contributions to chapter 3 – *Long-Term Vegetation Dynamics within the Hluhluwe iMfolozi Park*, which I co-authored with A. Carla Staver and Jan A. Graf. Section 2.3 includes my contributions to chapter 10 - *Interactions between Fire and Ecosystem Processes*, which I co-authored with Sally Archibald and others.

STAVER, A.C., BECKETT, H. and GRAF, J.A., 2017. Chapter 3. Long-Term Vegetation Dynamics within the Hluhluwe iMfolozi Park. *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*, p.56.

ARCHIBALD, S., BECKETT, H., BOND, W.J., COETSEE, C., DRUCE, D.J. and STAVER, A.C., 2017. Chapter 10. Interactions between Fire and Ecosystem Processes. *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*, p.233.

Chapter 2

Study Site

2.1. Hluhluwe iMfolozi Park

Field work for this research was conducted in the Hluhluwe-iMfolozi Park (28°12'41"S 31°59'31"E) in Northern Kwa-Zulu Natal, South Africa (Figure 2.1). The Hluhluwe-iMfolozi Park covers over 960 square kilometres of hilly countryside and is roughly divided by the Corridor Road into Hluhluwe Game Reserve in the North and iMfolozi Game Reserve in the South. Fieldwork was conducted in the Hluhluwe section of the park. Hluhluwe Game Reserve, one of the oldest reserves in South Africa, was proclaimed a protected area in 1895 by the Zululand Colonial Government to conserve a wildlife population ravaged by hunting.

Climate

Hluhluwe iMfolozi Park (HiP) has a coastally modified climate with much of the variability in local weather being related to topography. Mean annual precipitation is closely linked to altitude (Figure 2.1) in the park (Balfour and Howison 2001), producing a rainfall gradient from ~1000 mm per annum in the Hluhluwe section (580m a.s.l), to ~600 mm per annum in the iMfolozi section (70m a.s.l).

Annual rainfall is strongly seasonal with the majority falling during the warm summer months (October – March), whereas winter is characterized by cool, dry conditions punctuated by warm, dry conditions brought on by berg winds. Mean minimum and maximum temperatures in the Hluhluwe portion of the park are, respectively, 18 °C and 29 °C in summer (January) and 11 °C to 23 °C in winter (July) and are also strongly influenced by altitude.

Thunderstorms are a common feature of the summer rainfall season and lightning strikes occur in densities of approximately five ground-flashes per square kilometre per year (Ezemvelo KZN Wildlife, 2011). These strikes were probably the main source of ignition of fire in the region before significant human habitation occurred.

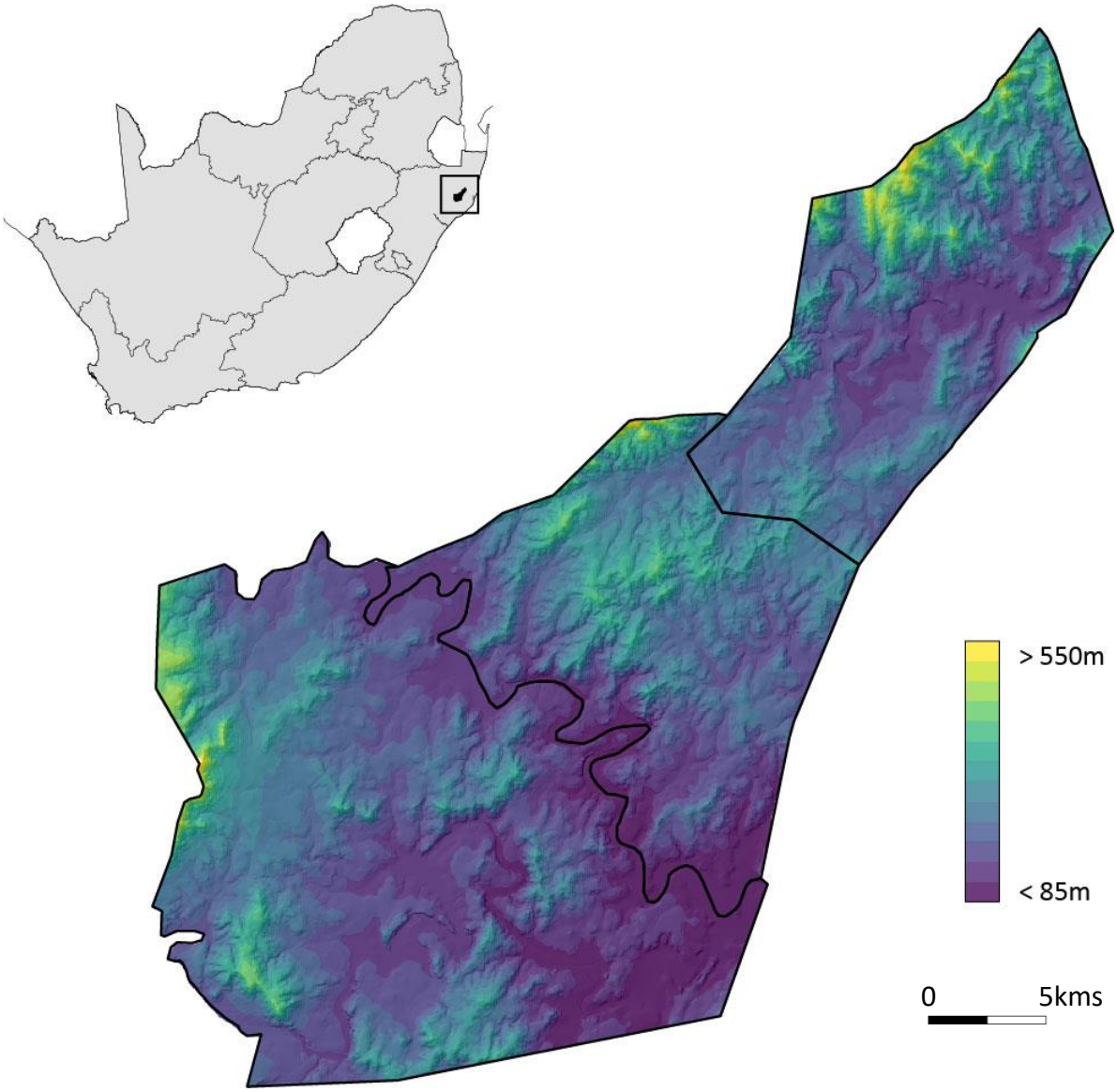


Figure 2.1. Elevation map of Hluhluwe iMfolozi Park. Inset shows the location of the park in South Africa. The park is roughly divided into three sections, Hluhluwe in the North, iMfolozi in the South and the Corridor between the two.

Geology and Soils

The southern African interior experienced two main periods of uplift during the Miocene and Pliocene, approximately 20 and 5 million years ago respectively (Partridge, 1998; Howison *et al*, 2017). The topography of HiP is shaped by the erosion after these events, with the main variation running North to South, perpendicular to the geomorphic tilting of the landscape (Howison et al, 2017) resulting in a high diversity of exposed geological substrates in the park (Downing, 1980; King, 1982). Catenary gradients, common in African savannas, are not present in Hluhluwe as a result of this complex topography and geology (Howison *et al*, 2017).

The geological substrates in Hluhluwe iMfolozi Park are predominantly from the Ecca Group within the Karoo Supergroup formation, with basalt intrusions in the northern region of Hluhluwe (Figure 2.2). The basalt substrates produce iron enriched structured Oxidic soils that are well drained and aerated, and relatively fertile whereas the Ecca sediments give rise to Duplex soils with marked clay enrichment and shallow Lithic soils overlaying weathered rock (Fey, 2010). Less common are the dark, fine textured Melanic soils and youthful Cumulic soils in the North of the park (Fey, 2010).

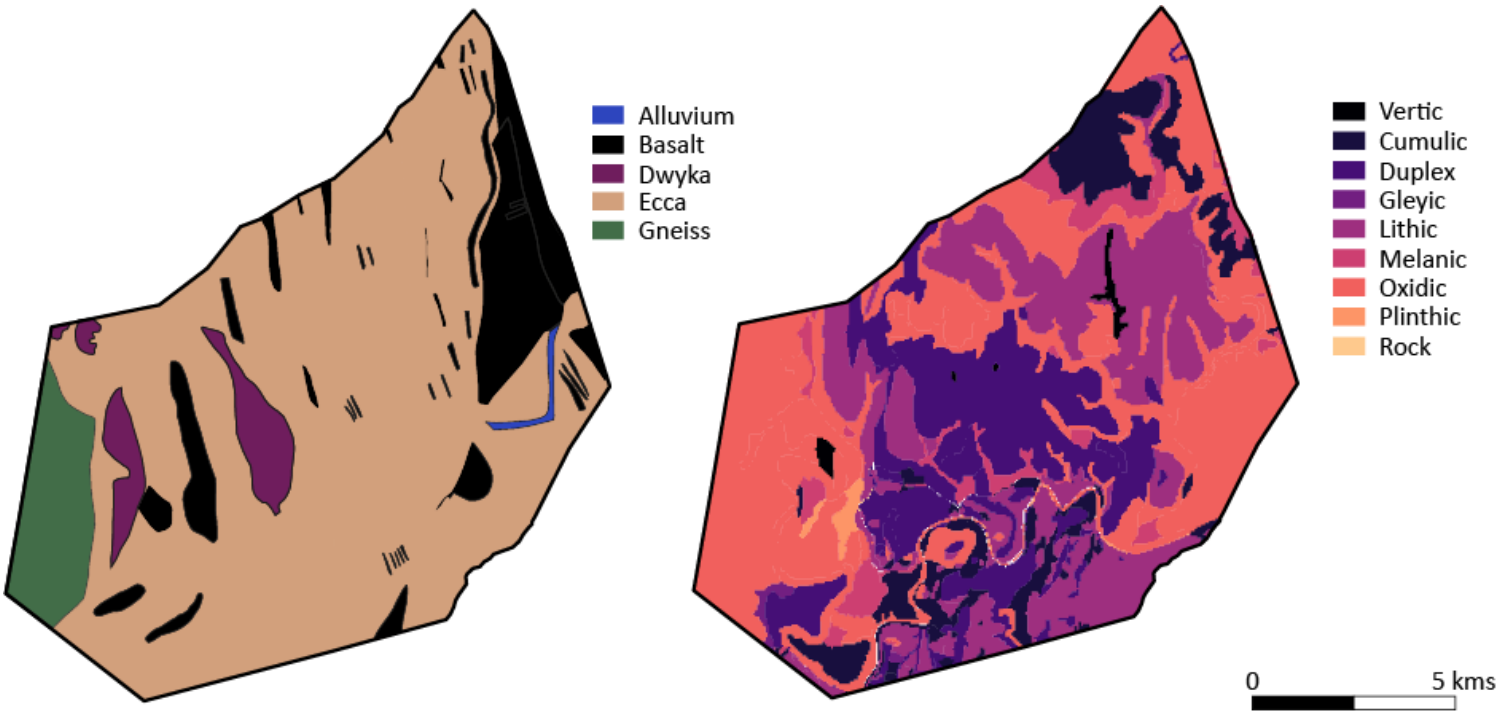


Figure 2.2. Geological maps of Hluhluwe Game Reserve showing (left) Geological Substrates, and (right) Soil Formations (Fey, 2010).

Early Human Habitation

Anatomically modern humans were present in the region as far back as 120 000 years ago, with evidence, such as rock paintings and stone tools, pointing towards habitation within the park (Penner, 1970; Mitchel, 2002). The impact of these hunter-gatherers on animal populations was most likely negligible, with most impact coming from modifications to fire regimes (Deacon and Deacon, 1999; te Beest *et al*, 2017). Iron Age farmers who arrived later were more prolific in their impact on the ecosystem through the harvesting of thatching grass, cultivation of crops, grazing by livestock (Hall, 1987; Huffman, 2007), harvesting wood for

fuel and housing and smelting of iron ore (Feely, 1980). During this period fires were probably lit before the end of the dry season, replacing lightning strikes as the dominant ignition source. Contrary to earlier assertions of savannas and grasslands as deforested or degraded landscapes (Acocks, 1953; Feely, 1980), carbon isotope ratios and palynological evidence points to the existence of these systems before the arrival of Iron Age farmers (West et al, 2000; Meadows and Linder, 1993, Gillson, 2015).

Fauna

While animal populations were decimated in the 19th century by hunting and by nagana outbreaks (animal trypanosomiasis) and eradication campaigns (1919 – 1954), a concerted conservation effort has brought back the full suite of megafauna. Current population densities of herbivores in the park (Table 2.1) are high and there is concern about the effects of megaherbivores, especially elephants, on woody vegetation (Druce et al, 2017). Staver et al (2009) show that browsing and fire together regulate and allow for the coexistence of trees and grasses in savannas. However, the effects of megaherbivores on savanna-forest boundary dynamics are overshadowed by the role of fire. This research is near unique in its analysis of the effects of extreme fires on mesic savanna-forest mosaic dynamics in one of the few 'natural' systems left in Southern Africa, however small the area.

Table 2.1. Mean herbivore populations within Hluhluwe iMfolozi Park between 1986 and 2008, with the exception of elephants (2014 helicopter survey) and hippos (approximate estimate). Data are from Owen-Smith et al (2017). Density (kg km^{-2}) is calculated using a mean body mass equal to three-quarters adult female body mass (Owen-Smith, 1988).

Common name	Scientific name	Diet Category	Population Total	Metabolic Density (kg km^{-2})
White Rhino	*Ceratotherium simum*	Grazer	1678	2228.6
Hippo	*Hippopotamus amphibius*	Grazer	30	43.4
African buffalo	*Syncerus caffer*	Grazer	4193	2096.5
Plain's zebra	*Equus quagga*	Grazer	2979	896.0
Waterbuck	*Kobus ellipsiprymnus*	Grazer	510	83.7
Blue wildebeest	*Connochaetes taurinus*	Grazer	2476	444.9
Warthog	*Phacochoerus africanus*	Grazer	2462	144.3
Common reedbuck	*Redunca arundinum*	Grazer	35	1.8
Mountain reedbuck	*Redunca fulvorufula*	Grazer	29	0.8
African elephant	*Loxodonta africana*	Mixed	698	2181.3
Nyala	*Tragelaphus angasi*	Mixed	6086	380.4
Impala	*Aepyceros melampus*	Mixed	13288	571.0
Black rhino	*Diceros bicornis*	Browser	230	215.6
Giraffe	*Giraffa camelopardalis*	Browser	600	492.2
Greater kudu	*Tragelaphus strepsiceros*	Browser	1186	194.6
Bushbuck	*Tragelaphus scriptus*	Browser	66	2.1
Grey duiker	*Sylvicapra grimmia*	Browser	645	12.6
Red duiker	*Cephalophus natalensis*	Browser	289	4.1
Steenbok	*Raphicerus campestris*	Browser	51	0.6
Blue duiker	*Cephalophus monticola*	Browser	6	< 0.1
Bushpig	*Potamochoerus porcus*	Omnivore	102	4.4

Vegetation definitions

HiP falls into the savanna biome of Southern Africa (Rutherford and Westfall, 1986) however the park comprises a mix of several vegetation types. Mucina and Rutherford (2006) classify the vegetation of Hluhluwe-iMfolozi Park as a mixture of Zululand Lowveld (SVI 23) occurring at the lower altitudes and Northern Zululand Sourveld (SVI 22) at the higher altitudes interspersed with patches of Eastern Scarp Forest (FOz 5).

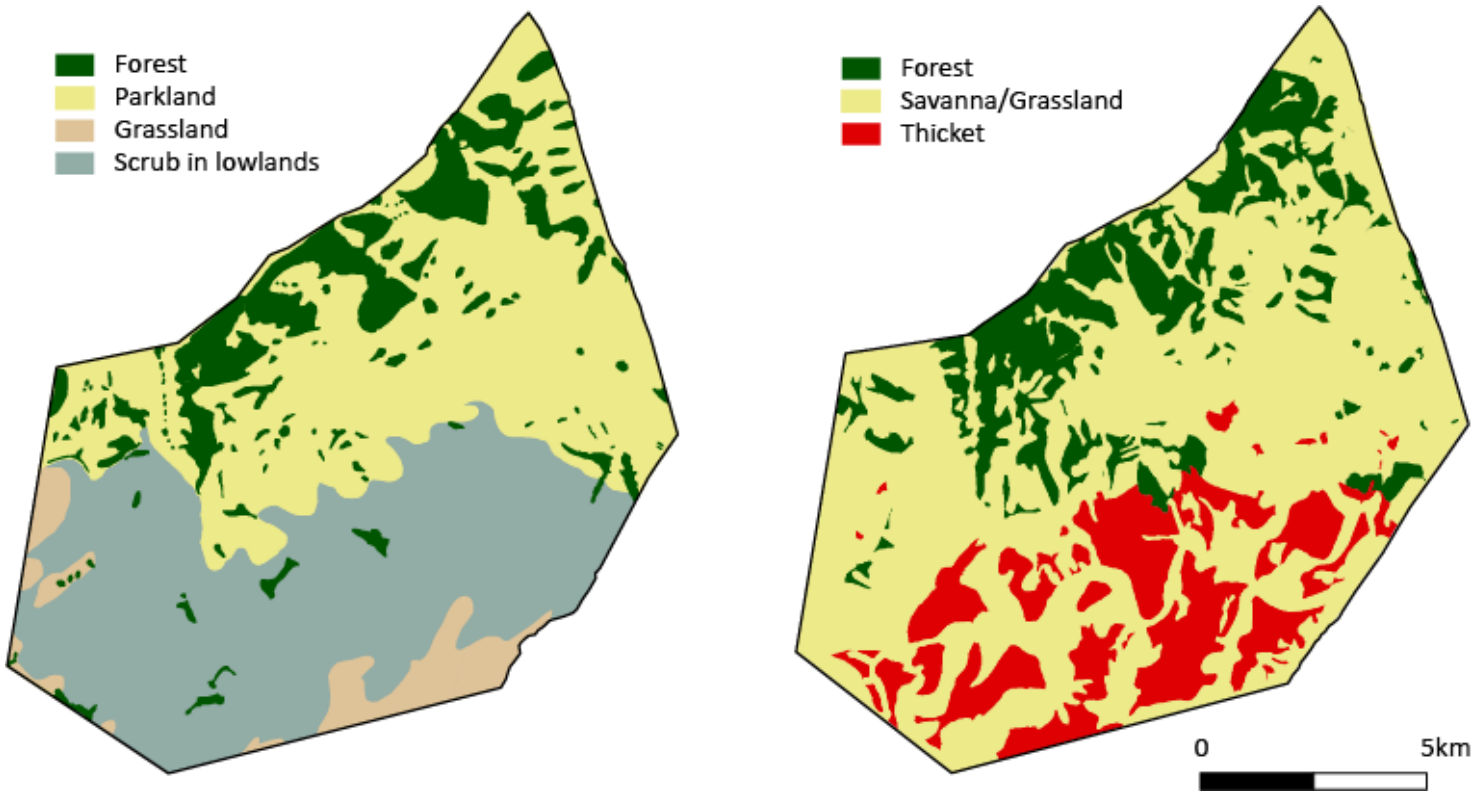


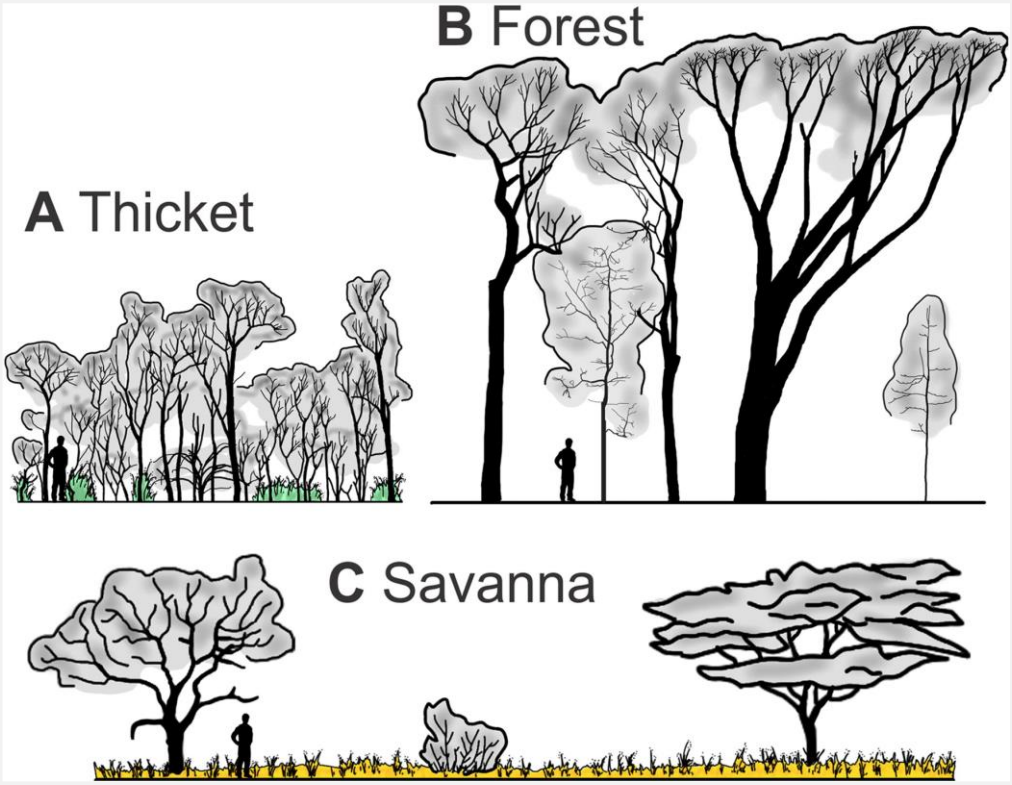
Figure 2.3. Vegetation maps of Hluhluwe Game Reserve (left) by Henkel (1937) and (right) Whateley and Porter (1983). Henkel - digitized and georeferenced by Heath Beckett for the HiP book. Whateley and Porter vegetation types have been reclassified according to Charles-Dominique et al (2015).

Definitions of vegetation types that occur in HiP have changed through time reflecting the ecological thinking of that period (Bews, 1921; Whateley and Porter, 1983). As equilibrium theories of plant succession and stable climaxes (e.g. Cowles, 1911; Clements, 1916) gave way to the more dynamic alternative stable state theory (e.g. Lewontin, 1969; May, 1977), grassland and savanna formations were no longer seen as degraded vegetation, rather, they

represent alternative states to forest and thicket formations - maintained by fire and herbivory (Bond and Parr, 2010; Ratnam *et al*, 2011).

The first account of vegetation types in the park by Henkel (1937) divided the vegetation of Hluhluwe Game Reserve into four units (Figure 2.3); forest, grassland, parkland and scrub. A later study by Whateley and Porter (1983) reports sixteen distinct woody plant communities; despite covering a larger area this still represents a massive increase in the diversity of vegetation units. The greatest confusion in all the classification schemes is over the definition, and ambiguous usage of, thicket vegetation. The term is used to describe encroached savanna as well as a distinct broadleaved thicket biome (Watson and Macdonald, 1983; Skowno *et al*, 1999; Brooks and Macdonald, 1983). There has been substantial debate about whether broadleaved thicket is a biome (e.g. as it is considered in Eastern Cape, chaco in South America), or whether 'thicket' should be used to refer to encroached savanna – a possible midpoint between savanna and forest (Parr *et al*, 2012). In this thesis I use the vegetation classifications of Charles-Dominique *et al* (2015), as displayed in Box 1.

Box 1. Hluhluwe iMfolozi Park Biome Definitions from Charles-Dominique et al (2015)



A) Thicket – "Dense shrub and treelet vegetation. The canopy is generally 4 to 6 m tall and varies from closed to fairly open. The understorey is variable with, usually, a dense layer of herbaceous sub-shrubs and shrubs but also occasional patches of shade-tolerant grasses."

B) Forest – "Woody tall (>10 m) vegetation with no C4 grass layer; forests have an intermediate shade-tolerant tree layer. The forest floor is usually a litter layer with occasional patches of herbaceous plants, including C3 grasses."

C) Savanna – "Discontinuous tree cover with a continuous layer of C4 grasses."

2.2. Vegetation Changes in Hluhluwe iMfolozi Park

Quantitative data on vegetation change during the last century in Hluhluwe iMfolozi Park are sparse. An examination of rates of recruitment of three prevalent *Acacia* species in the park from tree rings suggested that recruitment has been highly variable, potentially tied to variation in fire frequency and herbivore populations, and that species composition, at least within the *Acacia* community, may be changing drastically (see Figure 3 in Staver *et al.* 2011). Tree recruitment is not strongly cohorted and there is little evidence for the highly episodic tree establishment events documented elsewhere in Africa (Prins & van der Jeugd 1993). Similarly, a study examining community structure found evidence that Hluhluwe iMfolozi Park is undergoing major shifts in vegetation communities away from herbivore tolerant species towards fire-tolerant species (Bond *et al.* 2001).

Early Vegetation Studies

The earliest studies documenting vegetation change in the area focused on Hluhluwe Game Reserve (Brooks and MacDonald, 1983). During 1936, Henkel, at the behest of the Natal Provincial Council, investigated vegetation distributions in the HGR with the aim of improving the understanding of tsetse fly breeding habits (Downing, 1980). Henkel (1937) published a vegetation map of HGR (Figure 2.3) in which he described the vegetation of the park as predominantly open woodland and parkland. Pockets of forest were also noted in the North eastern section of the reserve. Despite acknowledgment of changes in vegetation (Attwell, 1948; Foster, 1955; Cowles, 1959), in particular the increase in wooded vegetation, the spread of *Acacia karroo* and other "undesirable plants" (Attwell, 1948), very little work was done to quantify these changes.

By comparing Henkel's 1937 and Downing's 1974 vegetation maps, Downing (1980) showed a 5% increase in forest area and an 8% decrease in grassland over the 36 year interval. This increase in wooded vegetation has since been confirmed through the use of aerial photographs (Watson and MacDonald, 1983; Watson, 1995). The trend is attributed to a number of factors including altered burning regimes and overgrazing (Watson, 1995). However more recent work comparing the park to adjacent communal and commercial lands

suggests that the woody increase is partly the result of global drivers, including changing rainfall distributions and increasing CO_2 (Wigley *et al.* 2010).

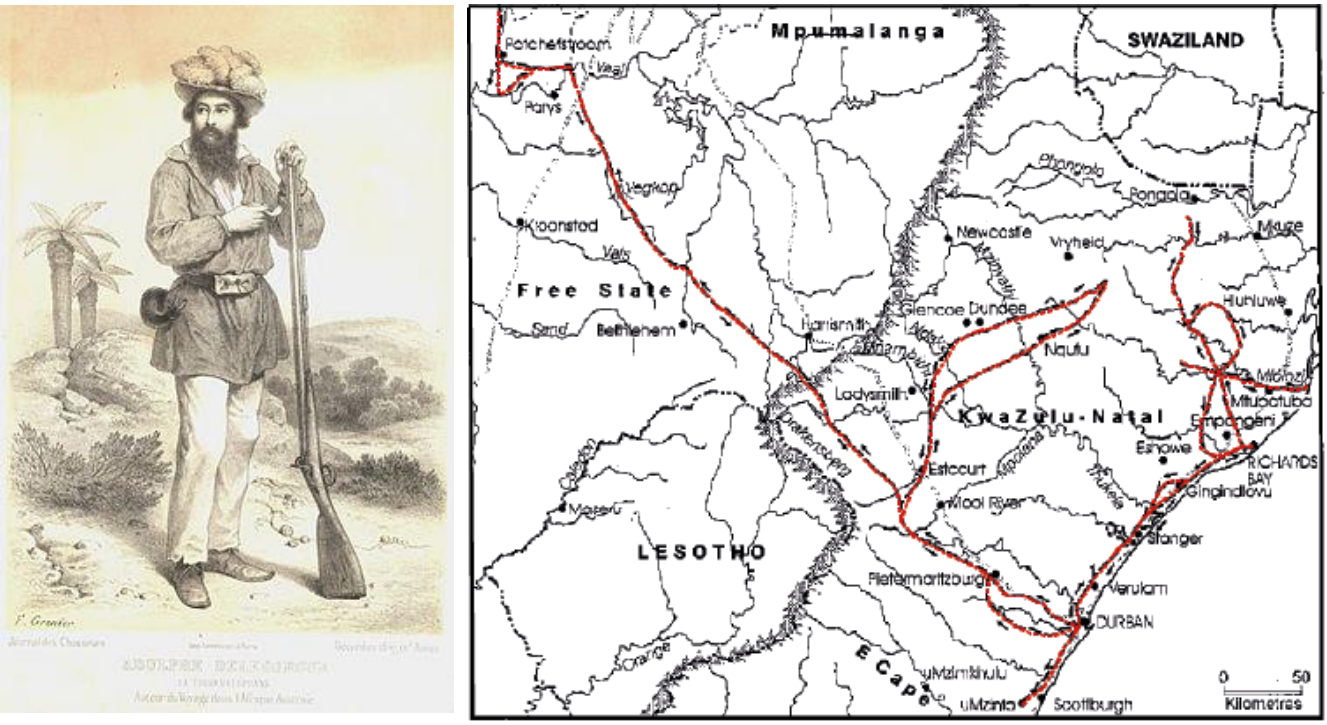


Figure 2.4. Portrait of Adulphe Delegorgue published in his *Voyage in Southern Africa* in 1847 (lithograph by F. Grenier) accompanied by a map of his travels (dotted red line) in KwaZulu Natal.

Historical Records and Anecdotes

Anecdotal evidence suggests similar trends in vegetation dynamics. From 1840 to 1842 Louis Adulphe Delegorgue (Figure 2.4), a French naturalist and big game hunter, frequented the area which would become Hluhluwe iMfolozi Park, in particular, the confluence of the White and Black iMfolozi River. Delegorgue, although not exempt from exaggeration and embellishment, provides one of the earliest accounts of the vegetation during that time. Delegorgue, whilst describing the course of White and Black iMfolozi Rivers, observed a "vast stretch of barren country", this area, from Nqolothi hill in the south-western corner of iGR right across to the current northern border of iGR, a distance of 20km, he later described as covered in "herbage" (i.e. not woody species). This area is currently covered by open and closed woodland and thicket, containing only a few isolated, small areas of grassland. Whilst hunting on the banks of the "Om-Philos-Om-Schlopu" (White iMfolozi River), Delegorgue

praises the open country for offering good visibility for hunting elephants, only to lament the lack of trees when he later encounters a lion.

There are however a number of accounts of "mimosas" (*Acacia spp*) dotting the landscape, as well as juveniles "which were hidden in the grass, [and] tore at our legs and so hindered our progress". Despite generally describing the vegetation as open, Delegorgue notes, on a number of occasions, thick bush and forested patches. The confluence of the White and Black iMfolozi is described as a "wooded region which abounds in game of all kinds". The forest and thicket patches described were in greatest abundance on steep mountain slopes and the banks of rivers were lined with "immense wild fig trees", "kruyz berries" (*Grewia occidentalis*) and tamboti trees. This pattern was also commented on by Aitken and Gale (1920) during a botanical survey to Zululand: "*The trees grow closest together along the country lying just beneath the western mountain boundary and near the river. All the trees found in the open veld are found growing along the rivers"*.

It is difficult to extract temporal trends in vegetation dynamics using anecdotal evidence. However a number of accounts of bush encroachment in Hluhluwe iMfolozi Park give credence to the notion that bush encroachment has occurred since the late 1800's. Aitken and Gale (1920) present an account of a resident in Hluhluwe valley who "*pointed to a hillside studded with thorn trees, and volunteered the information that in his child-hood there had not been one tree there*." Foster recorded from several old people in the iMfolozi area that they could not recall any areas encroached by woody vegetation in their youth (around the middle of the 19th century) (Foster 1955). Further in-depth discussions of vegetation changes follow in the rest of the thesis.

2.3. Fires and Firestorms

Fire History and Management

Little is known about the management of fire in Hluhluwe Game Reserve prior to its proclamation in 1895. However, as stated above, early human inhabitants made frequent use of fire for farming and as fuel in iron-smelting kilns, meaning fire was not limited to times of year when lightning strikes occur (Berry and MacDonald 1979). Between the proclamation of the park and 1930, fires in the park were managed in a similar manner, rangers simply set fires "whenever it seemed necessary" (Vincent 1970). Aitken and Gale (1921) noted the occurrence of winter fires in the region that would burn for a number of days and "as the country is not divided into farms, a single fire may rage for three days before it dies out."

Between 1930 and 1940 fires were actively suppressed to prevent burning the Harris traps deployed to combat tsetse fly. Aerial photographs taken in 1937 and recent work (Balfour and Howison, 2001; Archibald et al., 2010; Van Wilgen et al., 2004) dispute the fact that this management intervention achieved any significant reduction in total burned area. From 1955 onwards the fire program in the park was in the hands of the first Natal Parks Board ecologist CJ Ward, who initiated controlled burning for various management objectives, and the detailed recording and mapping of fire events (Figure 2.5) which still continues today (Berry and MacDonald 1979). During this period controlled burns were applied with two main objectives - protection and promotion of fire-sensitive plants and maintenance of fire-induced seral communities (Porter 1977 in Berry and MacDonald 1979). The rangers were also encouraged to assess fuel loads and to apply more controlled burns after periods of high rainfall.

In the 1970's Roger Porter, the regional ecologist, promoted burning to remove moribund grass material, prevent woody thickening, and move grazers from heavily-utilised bottomlands into the newly-burned veld to prevent soil degradation. Porter and his colleagues also tried to implement a more varied season and frequency of burning. This was not met with enthusiasm from rangers who had generally been schooled in an agricultural approach to fire focussed on applying fires to preserve soil and the climax grass communities thought to be good for cattle. The practice of only burning after the spring rains – and avoiding

annual burns - was pervasive in Natal due to the influence of Professor J. D. Scott (1959) from the Natal University Pasture Science Department, and became law in the mid-1970s. The motivation for this was that early-season burns exposed the soil to erosion, and reduced productivity of the grass sward (Tainton et al, 1977). Despite questions from ecologists and farmers about the wisdom of this approach (Tainton et al, 1977) this was the default fire application throughout the 1970's and 1980's.

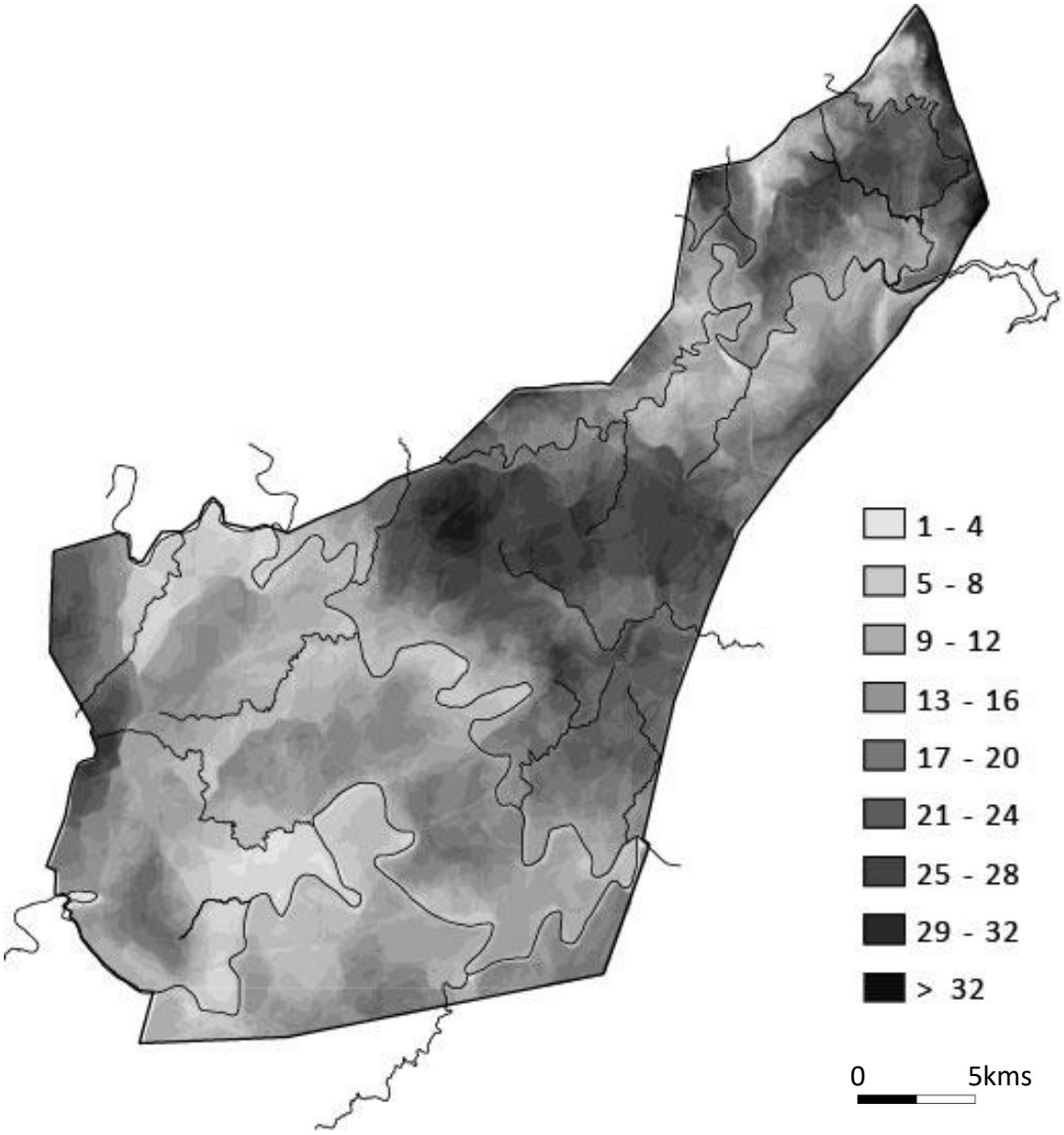


Figure 2.5. Number of fires in Hluhluwe iMfolozi Park between 1955 and 2013 (data from Ezemvelo KZN Wildlife). Fire records are hand drawn by section rangers of HiP and as a result do not identify small fire refugia or unburnt vegetation patches. Darker regions indicate more fires.

The number of prescribed burns annually peaked in the 1990's, with the initiation of patch-mosaic burning, aimed at increasing spatial heterogeneity in fire regimes and vegetation communities (Parr and Anderson, 2006).The latest HiP Integrated Management Plan (2011) states quite broadly that 'the intention of fire management in HiP is to 'actively manage for a shifting mosaic of differing fire impact and size, thereby creating a diversity of habitats that should ensure the conservation of the biodiversity representative of the area'.

Firestorms

To understand the ecological effects and implications of firestorms it is important to first define what is meant by the term firestorm and how these events differ from 'typical' fires. The extent and severity of a fire are controlled by a number of biotic and abiotic factors that range in both temporal and spatial scale (Bond and Keeley, 2005), which leads to a degree of variability even within single fire events. The terminology used in fire ecology can often cause confusion – e.g. the usage of fire intensity versus fire severity (Keeley, 2009) – and a number of terms exist to describe different components of the fire regime such as the type of fire (surface, ground and crown fires, which classify the source of fuel and location of the fire). A 'typical' fire is constrained by its fire environment (wind speed, fuel availability and moisture content, topography). Firestorms, on the other hand, are powerful enough to influence and alter the fire environment. A firestorm is an extreme natural phenomenon which occurs when a fire achieves an intensity at which it starts to generate its own wind system, a convective column caused by warm rising air, which draws in oxygen and fuels a particularly intense fire.

Savanna fires, characteristically, do not cross the boundary into forest due to a sudden reduction in fuel, as shade intolerant C4 grasses disappear within meters of the boundary from savanna or grassland into thicket or forest (Hennenberg et al. 2006; Hoffmann et al. 2012; Charles-Dominique et al, 2018). The lack of grassy fuel is usually sufficient to prevent a fire from burning into a thicket or forest. Forests and thickets also alter the microclimate, reducing wind speeds and increasing fuel moisture (Biddulph and Kellman, 1998; Little et al., 2012; Ibanez et al, 2013) further reducing the likelihood of fire. Firestorms, however, have no difficulty in crossing the boundary between biomes.

Figure 2.6. Fires in Hluhluwe iMfolozi Park, left, Firestorm in September 2008 (photograph by Dirk Swart) and, right, a 'typical' fire July 2014 (photograph by Heath Beckett).

On the 14th and 15th September 2008 a firestorm occurred (Figure 2.6) in the Hluhluwe section of the park and, unlike typical savanna fires, it tore through vast tracts of thicket and forest. Events such as this are both rare and extreme which makes studying them, and the conditions necessary for their formation, difficult. Pioneering work, conducted in HiP, has helped to identify the conditions under which firestorms are thought to develop using the framework of Bradstock (2009). He identified a set of 'switches' that need to be 'flipped on' for a fire to occur, and a modified set of switches was developed for firestorms (Browne and Bond, 2011). An analysis of the weather conditions preceding and during the 2008 fire gave rise to a set of switches known as 30' 30' 30' conditions which allowed a surface fire to transition to an intense crown fire. Provided there is sufficient fuel that is adequately cured, a firestorm will develop if these three switches are 'flipped on'; the air temperature is above 30°C, the relative humidity is below 30% and wind speeds gusting to 30km/h or more (Browne and Bond, 2011).

The savanna-thicket-forest mosaic of HiP is a choice example of alternate vegetation states that can occur under the same climatic conditions. The majority of the work done on savanna-forest-thicket mosaics, in the context of the Alternative Stable States hypothesis, focuses on positive and negative feedback loops and how this affects the bistability of these systems. Firestorms, however, appear to be an example of a 'regime shift' providing a destabilizing mechanism which could act as a driver of abrupt biome level change. Three major firestorms have occurred in Hluhluwe iMfolozi Park since the beginning of this millennium. This is in

contrast to the last century where there is scant evidence of firestorms occurring, as demonstrated by the overwhelming bush encroachment in the park since the 1930s (Wigley et al, 2009). As stated earlier, these fires are unique in that, with relative ease, they crossed the boundary from savannas to closed woody vegetation, thereby switching fuel types from highly flammable grasses to forest leaf litter, understorey shrubs and herbs, and woody biomass. This effectively opened up the environment through the widespread mortality and topkill of adult trees (Browne and Bond, 2011).

Once the smoke had cleared, it became apparent that these high intensity fires might be the solution to the problem of colonisation of savannas by thicket and forest vegetation. Patches of thicket vegetation, dominated by *Euclea racemosa, Euclea divinorum, Berchemia zeyheri* and *Sideroxylon inerme*, with sparse grass cover, showed a significant structural change following the 2008 firestorm with 21% mortality of adult trees (Browne and Bond, 2011). These patches were quickly colonised by grasses and accumulated enough fuel to burn again in 2010, 2012 and 2014 (EKZNW), a fire return interval which is indicative of savanna vegetation. There is concern however over whether or not this indicates a biome shift. Follow up work in 2012 demonstrated that the dominant trees in these areas are not savanna trees but simply basally resprouting thicket species such as *E. racemosa* and *E. divinorum* (Wills, unpublished thesis). The growth rate of these resprouts is higher than that of seedlings due to existing underground storage (Bellingham and Sparrow, 2000). Once the ecosystem has had a sufficient fire free interval to allow canopy closure, the flammable grassy layer is shaded out and the system could return to its original state. This implies that although firestorms can precipitate a change, effective management of the area is needed to complete the switch from thicket to savanna through subsequent fires and grazing.

Chapter 3

Safety first, then teamwork

A landscape scale investigation of the drivers of forest persistence in fire-prone mesic savannas

3.1. Abstract

Does complex topography facilitate the establishment and persistence of fire sensitive (forest) vegetation in a fire prone landscape? Fire sensitive vegetation is predicted to establish and persist in areas where the fire return interval is lower due to a topographic hindrance on fire spread. Using aerial photographs from six time periods between 1937 and 2013, I mapped vegetation changes in Hluhluwe iMfolozi Park. Using a Generalized Additive Model (GAM) I built a Habitat Suitability Index (HSI) map based on topographic variables related to fire behaviour and the vegetation distribution maps. I investigated transitions between time periods based on the HSI map, as well as the effects of neighbourhood on transition probabilities. Forest cover has increased since 1937, however this has not been a linear increase with a peak in extent in the early 1990's. The habitat suitability index, using topographic predictors associated with fire behaviour, relates to the expansion and contraction of forest vegetation (safety first). The expansion and contraction dynamics are however more nuanced, with the *in situ* vegetation neighbourhood playing a large role (teamwork). Forest distributions in HiP have not remained static over time and have expanded into areas that were once savannas. This is a dynamic system where both forest and savanna boundaries can change considerably. Fire refugia are important for the long term persistence of forests in fire prone landscapes.

Keywords: fire, forest, savanna, generalized additive model, habitat suitability index, refugia, Alternative Stable States

3.2. Introduction

At a landscape scale, interactions between fire and vegetation often result in a mosaic of fire-adapted (e.g. savannas and fynbos) and fire-sensitive (e.g. forests) vegetation communities (Hoffmann et al, 2009). The biomes in these mosaics are recognised as alternative stable states, such that a given set of environmental conditions can support either biome in a stable, non-transitory state (Scheffer and Carpenter, 2003; Hirota et al, 2011). This is highlighted in regions where open grasslands and savannas occur in the presence of dense forests, creating landscape mosaics with abrupt boundaries between vegetation types (Warman and Moles, 2009). Examples of these vegetation mosaics are found in Brazil (Hoffmann et al, 2009), Ghana (Markham and Babbedge, 1979; Swaine, 1992), the Central African Republic (Beauvais, 2009), Ivory Coast (Goetze et al, 2006; Hennenberg et al, 2006), India (Mariotti and Peterschmitt, 1994; Puyravaud et al, 1994), Madagascar (Virah-Sawmy, 2009), New Caledonia (Perry and Enright, 2002; Stevenson and Hope, 2005) and Australia (Bowman, 2009).

The majority of the research on alternative stable states however is at a global or continental scale which tends to gloss over the local scale controls of vegetation state. Lehmann *et al* (2011) presented a range of environmental conditions in which savannas occur; however, they also state that "some proportion of the land is always not-savanna". This implies savannas are not deterministically defined by these conditions and local scale modifications may play a role in the presence of savanna-forest mosaics. At a global scale, the role of topographic complexity in determining savanna distribution is minimal (Archibald *et al*, 2009; Lehmann *et al*, 2011). However, at a smaller scale of investigation, the effect of topography on fire behaviour may play a much larger role in facilitating the growth and persistence of closed canopy (forest) vegetation in fire refugia (Geldenhuys, 1994; Clarke, 2002). An understanding of fire spread and behaviour on complex terrain could provide insight into the presence and persistence of these enigmatic forest patches in a fire-prone ecosystem and shed new light on the 'top-down' versus 'bottom-up' control debate of alternative stable states in these vegetation mosaics.

The mesic savanna-forest-thicket mosaic in Hluhluwe-iMfolozi Park, north eastern South Africa, is a prime example of these vegetation mosaics. Within HiP we find a mosaic of open

(savanna and grassland) and closed (forest and thicket) vegetation types with distinct species assemblages (Charles-Dominique et al, 2015). The boundaries between vegetation types are abrupt, resulting in a complete shift in tree density and species composition over the scale of a few meters. Ecological and physiological differences between these suites of species play a dominant role in vegetation responses to fire at both an individual and biome level and affect the distribution of the different vegetation types (Hoffmann et al, 2012a; Charles-Dominique et al, 2015). Evidence from soil Carbon isotope ratios indicate the presence of ancient grassland/open habitats under current forest distributions (West et al, 2002) with forests diminishing to a local minima during the last glacial maximum (Eeley *et al*, 1999). How then, did forests establish and persist in an area with a long history of fire?

It is widely accepted that positive feedback loops with fire maintain forest and savanna patches in these mosaics (Beckage and Ellingwood, 2008; Geiger *et al*, 2011; Staver et al, 2011). Experimental exclusion of fires in mesic savannas is usually followed by an increase in woody biomass and an increase in forest species which is used as evidence for alternative stable states (Warman and Moles, 2009; Hoffmann *et al*, 2012; Murphy and Bowman, 2012). Here, we ask how the abiotic template affects the expansion and contraction of closed canopy vegetation through local scale modifications of the fire regime. In particular, I am interested in how topography influences fire spread and how that, in turn, influences forest distribution. If these topographic modifications are indeed important for forest vegetation, fire refugia - areas where the occurrence of fire is lower than the surrounding matrix - should offer a higher chance of forest tree survival, establishment and persistence (Geldenhuys, 1994, Clarke, 2002).

While the topography of Hluhluwe has remained relatively constant over time, there have been large changes in extrinsic drivers affecting vegetation dynamics, especially different fire management strategies and global change drivers such as increased atmospheric CO_2 and nitrogen deposition. A century ago, Aitken and Gale (1921) documented large fires burning in the region: *"Scarcely a night during winter but that a grass fire is seen somewhere on the veld, and as the country is not divided into farms, a single fire may rage for three days before it dies out".* Archibald et al (2017) highlighted a diverse suite of fire management strategies employed in the park, with fire management before the 1930's defined by "*whenever it seemed necessary*" by the game conservator. This was followed by complete fire suppression

in order to protect Harris traps used to control an outbreak of tsetse fly. Active fire management started in 1955. Active fire management objectives have ranged from attracting game and increasing visibility for tourists, preventing soil erosion by burning after the first spring rains in the 1970s and 1980s, to patch-mosaic burning to increase heterogeneity from the 1990s onwards. Wigley et al (2009) noted an overall increase in woody vegetation within Hluhluwe between 1937 and 2004, as well as in the surrounding communal and commercial lands, and attributed this to global drivers such as increases in CO_2 and, possibly, atmospheric nitrogen deposition.

The temporal and spatial effects of these changes are difficult to disentangle from one another, hampering our understanding of the patterns and rates of change in the system (Brook and Bowman, 2006). Here I analyse the spatial and temporal dynamics of the distribution of open and closed canopy vegetation types within Hluhluwe Game Reserve from 1937 to 2013 using a correlative modelling approach based on aerial photographs, early vegetation maps (Henkel, 1937; Whateley and Porter, 1983) and the topographic template of the park. Does complex topography facilitate the establishment and persistence of fire sensitive (forest) vegetation in a fire prone landscape?

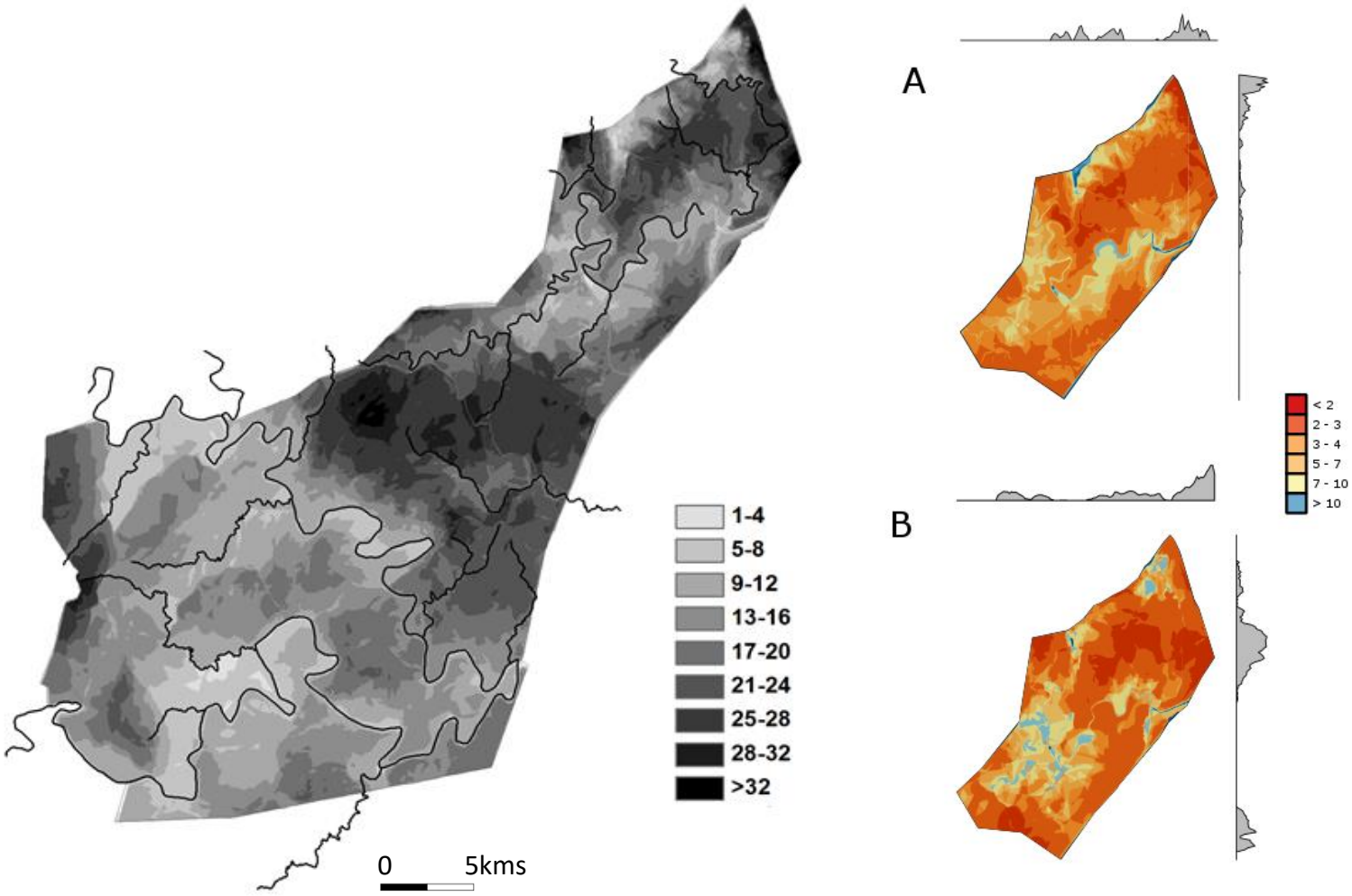


Figure 3.1. Fire Frequency map (left) of Hluhluwe iMfolozi Park from 1955 to 2013 and Fire Return Interval maps (right) for Hluhluwe Game Reserve for two different time periods. A) 1955 to 1992, during which time closed canopy coverage nearly doubled (10.8% to 19.3%), and B) 1993 to 2013 when closed canopy coverage decreased (19.3% to 14.1%). See Table 3.1 for values. Margin plots for A and B show the density of cells with a fire return interval less than two years.

3.3. Materials and Methods

Study Area

Hluhluwe-iMfolozi Park (28°12'41"S 31°59'31"E), situated in Northern Kwa-Zulu Natal, South Africa, covers over 960 square kilometres of hilly countryside. The park has a coastally modified climate with much of the variability in local weather being related to topography (Ezemvelo KZN Wildlife, 2011). Mean annual precipitation is closely linked to altitude in the park (Balfour and Howison 2001), producing a rainfall gradient from ~1000 mm per annum in the Hluhluwe section (580m a.s.l), to ~600 mm per annum in the iMfolozi section (70m a.s.l). Annual rainfall is strongly seasonal with the majority falling during the warm summer months (October – March), whereas winter is characterized by cool, dry conditions punctuated by warm, dry conditions brought on by berg winds. Mean minimum and maximum temperatures in the Hluhluwe portion of the park are, respectively, 18 °C and 29 °C in summer (January) and 11 °C to 23 °C in winter (July) and are also strongly influenced by altitude. Thunderstorms are a common feature of the summer rainfall season and lightning strikes occur in densities of approximately five ground-flashes per square kilometre per year (Ezemvelo KZN Wildlife, 2011).

Mapping closed canopy vegetation

In order to assess the spatiotemporal dynamics of vegetation change in HiP I produced maps of closed canopy vegetation from a chronological sequence of historical aerial photographs. The aerial photographs, obtained from the National Geo-spatial Information (NGI) office, spanned from 1937 to 2013 and included ten time periods. Six of these (1937, 1960, 1975, 1992, 2006 and 2013) were selected based on photo quality and to provide the most regular time intervals possible. The 2006 and 2013 images were the highest quality images and were ortho-rectified by the NGI. The 1937 to 1992 images were scanned and resampled to a pixel resolution of $1m^2$, mosaicked and geo-referenced to the 2013 images using QGIS Pisa. The average horizontal root mean square errors were less than 15 m for these time periods and the average root mean square error was 7.25 m.

A grid, with cells 10m x 10m, was draped over the mosaicked images and each cell was manually classified as either closed canopy vegetation (F) or open vegetation (S) with a value

of 1 and 0 respectively (Figure 3.4). For cells that contained both vegetation types, those with more than 50% tree cover were classified as closed canopy. The classifications were visually compared to vegetation maps of HiP by Henkel (1937) and Whateley and Porter (1983) using the vegetation definitions provided in Box 1. The spatial resolution of the classified images was degraded to 30m x 30m to match that of the ASTER Global Digital Elevation Model (DEM). The vegetation maps were restricted to Hluhluwe Game Reserve, rather than HiP as a whole, as only Hluhluwe Game Reserve was mapped by Henkel (1937).

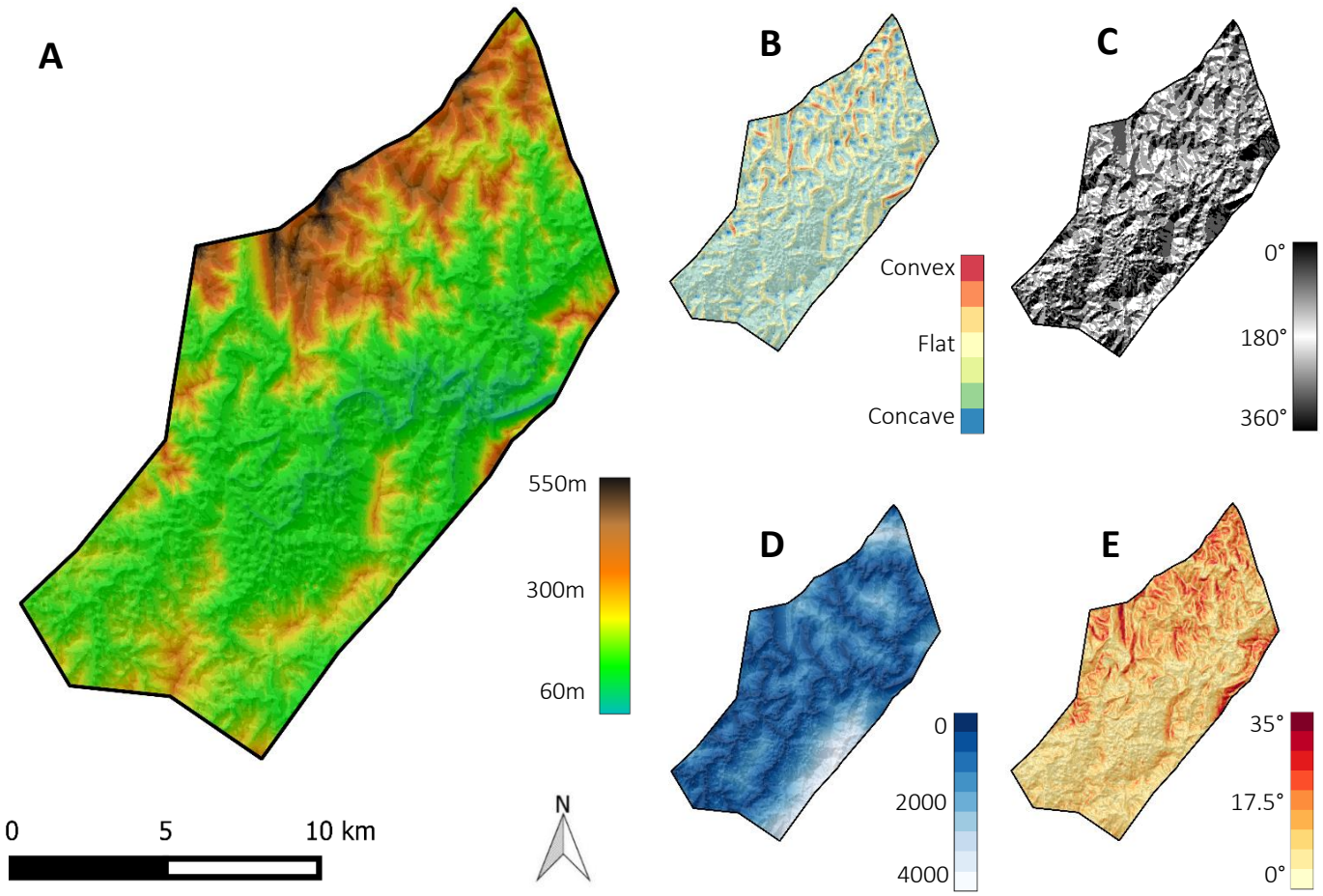


Figure 3.2. Topographic variables used in the construction of the Habitat Suitability Index for Hluhluwe Game Reserve, A) Elevation, B) Curvature, C) Aspect, D) Distance to Nearest River, and E) Slope. Elevation data come from the ASTER GDEM product. The remaining variables (with the exception of the distance to nearest river) were calculated from this layer in QGIS. Scale bar displays the scale of A.

Closed Canopy Cover in Relation to Topographic Variables

The classified images, indicating presence and absence of closed canopy vegetation, were compared across the different time periods, identifying periods and rates of expansion and contraction. To investigate the spatial aspect of the vegetation dynamics I calculated the mean percentage and standard deviation of closed canopy coverage in a range of classes for each of the topographic variables; Aspect, Elevation, Curvature, Slope and the Distance to the Nearest River (Figure 3.2). These topographic raster layers were calculated in QGIS Pisa based on the 30m resolution ASTER GDEM, with the exception of the distance to rivers. This was calculated as the distance of each cell to the nearest of the four main rivers in Hluhluwe (Mansiya, Manzibomvu, Nzimane and Hluhluwe Rivers) and their tributaries. The smallest tributaries (1st order streams) were not included in the analysis as they were too small to have had an effect on fire spread. As discussed, there is an interaction between the topographic variables (and the associated effects on fire behaviour) and wind direction (See Brook and Bowman (2006) and Table 1 in Ibanez et al (2013) for details on these effects). Low exposure to solar radiation leads to reduced evapotranspiration, and so increased soil and fuel moisture (Mackey et al, 2002). Fire intensity is lower on areas with lower solar radiation, shaded aspects (Bradstock, 2010). Fires burning upslope have a decreased angle between the flame and the fuel, which leads to an increase in preheating of fuels and an increased rate of spread. The opposite occurs when fires are burning downslope – the radiant heat transfer decreases (Burgan and Rothermel, 1984; Trollope, 1984). The prevailing wind direction during the fire season is a northerly to north-easterly wind (See Chapter 4), so the relationships between closed canopy coverage and the topographic variables (excluding Aspect) were attained using a North and South Facing subset of the data.

Closed Canopy Habitat Suitability Map

I constructed a habitat suitability index for closed canopy vegetation using a species distribution model based on the data obtained from the aerial photographs. The habitat suitability index (HSI) provides an estimated probability of the presence of closed canopy vegetation in each cell across the landscape, a prediction that is based on the presence of closed canopy vegetation in cells with similar values for the predictor (topographic) variables. Based on the selected predictor variables (Figure 3.2), the HSI can be seen as an "*index of*

topographic fire protection" (Brook and Bowman, 2006). An HSI was calculated for each of the time periods based on the topographic predictor variables and the aerial photograph derived vegetation maps for the specific time periods. A map of predicted HSI values was created for each time period based on these models and an average of these six maps was used in the analyses.

The model was constructed using Generalised Additive Models (GAMs), which are an extension of Generalized Linear Models (GLMs), both of which are particularly well suited to species distribution modelling of presence-absence data (Guisan, 2002; Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). I selected a GAM, as opposed to a GLM, as the assumption of a linear relationship between the response and explanatory variable is void. GAMs allow for nonparametric smoothing splines to be fitted to the covariates which allows for a more accurate representation of the response curve (Elith and Burgman, 2003). For example, a cyclic cubic spline was fitted to the Aspect variable as the minimum (0°) and maximum values (360°) represent the same aspect.

For the remaining covariates, the GAM approach did not require *a priori* predictions of one parametric form or another (Crawley, 2007). This, in conjunction with the selection of variables based on expert knowledge, and not a stepwise selection process, avoids over-fitting of models. I built the models in R with the *mgcv* package (Wood, 2001), using a binomial probability distribution and logit-link function, similar to that of Ibanez *et al* (2012). Latitude and Longitude were modelled explicitly in the GAM to account for spatial autocorrelation. The dataset was randomly divided into calibration (70%) and validation (30%) datasets, and the model was trained using the calibration dataset and the potential for extrapolation was tested on the validation dataset (Guisan and Zimmermann, 2000) using the D^2 statistic for goodness of fit and the Kappa index to measure the accuracy of predicted versus observed results (Cohen, 1960).

Expansion and Contraction of Closed Canopy Vegetation

I constructed a transition matrix between each time period where the proportions of cells of each vegetation type within habitat suitability classes were used to calculate the probability of transitioning from one state to another versus remaining in the same state (Ibanez et al, 2013; Brook and Bowman, 2006; Augustine et al, 2001). I performed OLS regressions on the

transition probabilities of open and closed vegetation types within different habitat suitability classes for each time period to compare the shapes and slopes of the curves to one another in relation to fire management practices during these time periods.

Fire effects are inherently spatially variable with the majority of fires burning up to a forest edge and no further. This implies the trees on the edges of forests are those most likely to burn whereas a forest tree surrounded by forest trees is less likely to burn. I investigated the effects of each cell's neighbourhood matrix through a neighbourhood index. For each cell, in each time period, I calculated an index of neighbourhood protection based on the number of neighbouring cells containing closed canopy vegetation. The neighbourhood index was defined as the sum of cells, classified as closed canopy vegetation, within 60 meters of the focal cell, with an exponentially decreasing weighted value based on the distance from the focal cell. I then analysed the effects of this neighbourhood protection index on the vegetation transition probabilities for four different habitat suitability classes between each time period.

3.4. Results

Closed canopy vegetation increased in extent from 2362 hectares in 1937 to 3073 hectares in 2013 (Table 3.1). The maximum extent however was in the 1990's when approximately 4200 hectares (almost 20%) of Hluhluwe Game Reserve was classified as closed canopy environment, with subsequent loss from 1992 to 2013. The earliest time period (1937 - 1960) shows a higher increase of closed canopy vegetation on North facing aspects, compared to that on South facing aspects. This is in contrast to the following two periods of closed canopy increase where most gain was on the South facing aspects. From 1992 to 2013, South facing aspects lost more cover than North facing aspects. Of particular interest is the final time period where more than 100 ha closed canopy vegetation was lost on average per year, the majority being burnt in three major fires in 2004, 2008 and 2012 (See Chapter 5).

Table 3.1. Changes in Closed Canopy Coverage in Hluhluwe Game Reserve between 1937 and 2013 based on aerial photograph classification. Maps shown in Figure 3.4.

Year	Area	Closed Canopy Cover		Absolute Change		Relative Change	
		(ha)	(%)	(ha)	(%)	(ha.yr^{-1})	(%.yr^{-1})
1937	North-facing	406.1	1.86	-	-	-	-
	South-facing	1956.3	8.97	-	-	-	-
	Total	2362.4	10.83	-	-	-	-
1960	North-facing	437.0	2.00	30.9	0.14	1.3	0.01
	South-facing	1977.0	9.06	20.7	0.09	0.9	<0.01
	Total	2414.0	11.07	51.6	0.24	2.2	0.01
1975	North-facing	497.3	2.28	60.3	0.28	4.0	0.02
	South-facing	2263.1	10.38	286.0	1.31	19.1	0.09
	Total	2760.3	12.65	346.3	1.59	23.1	0.11
1992	North-facing	1065.6	4.89	568.4	2.61	33.4	0.15
	South-facing	3134.9	14.37	871.8	4.00	51.3	0.24
	Total	4200.5	19.26	1440.2	6.60	84.7	0.39
2006	North-facing	936.9	4.30	-128.7	-0.59	-9.2	-0.04
	South-facing	2934.8	13.45	-200.1	-0.92	-14.3	-0.07
	Total	3871.7	17.75	-328.8	-1.51	-23.5	-0.11
2013	North-facing	582.0	2.67	-354.9	-1.63	-50.7	-0.23
	South-facing	2491.0	11.42	-443.8	-2.03	-63.4	-0.29
	Total	3073.1	14.09	-798.7	-3.66	-114.1	-0.52

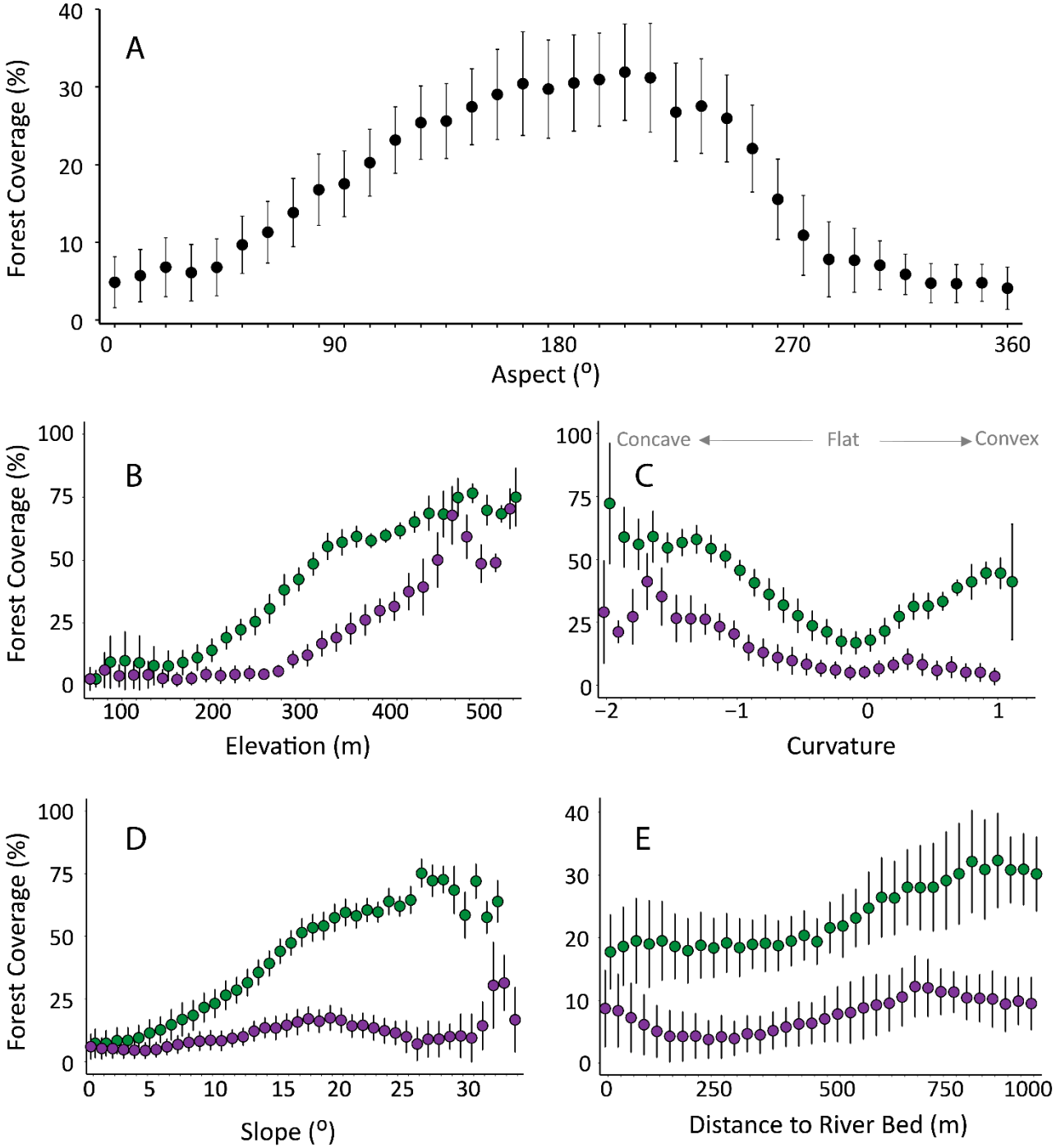


Figure 3.3. Closed Canopy Coverage in relation to the topographic variables used in the construction of the Habitat Suitability Index. A) Aspect, B) Elevation, C) Curvature, D) Slope and E) Distance to River Bed. For B-E, closed canopy coverage is calculated for North (Purple) and South (Green) facing slopes. Error bars indicate standard deviation between time periods.

The distribution of areas with a high fire return interval (< 2 years) for these two periods shifted from the edges of the park in the initial time period to the centre of the park in the later time period (Figure 3.1). Despite this, there was no significant change in overall fire return intervals, or the areas burnt at least every two years. The notable difference between

these two periods is the occurrence of firestorms. There is little (no?) evidence of firestorms in the park fire records prior to the 1990's.

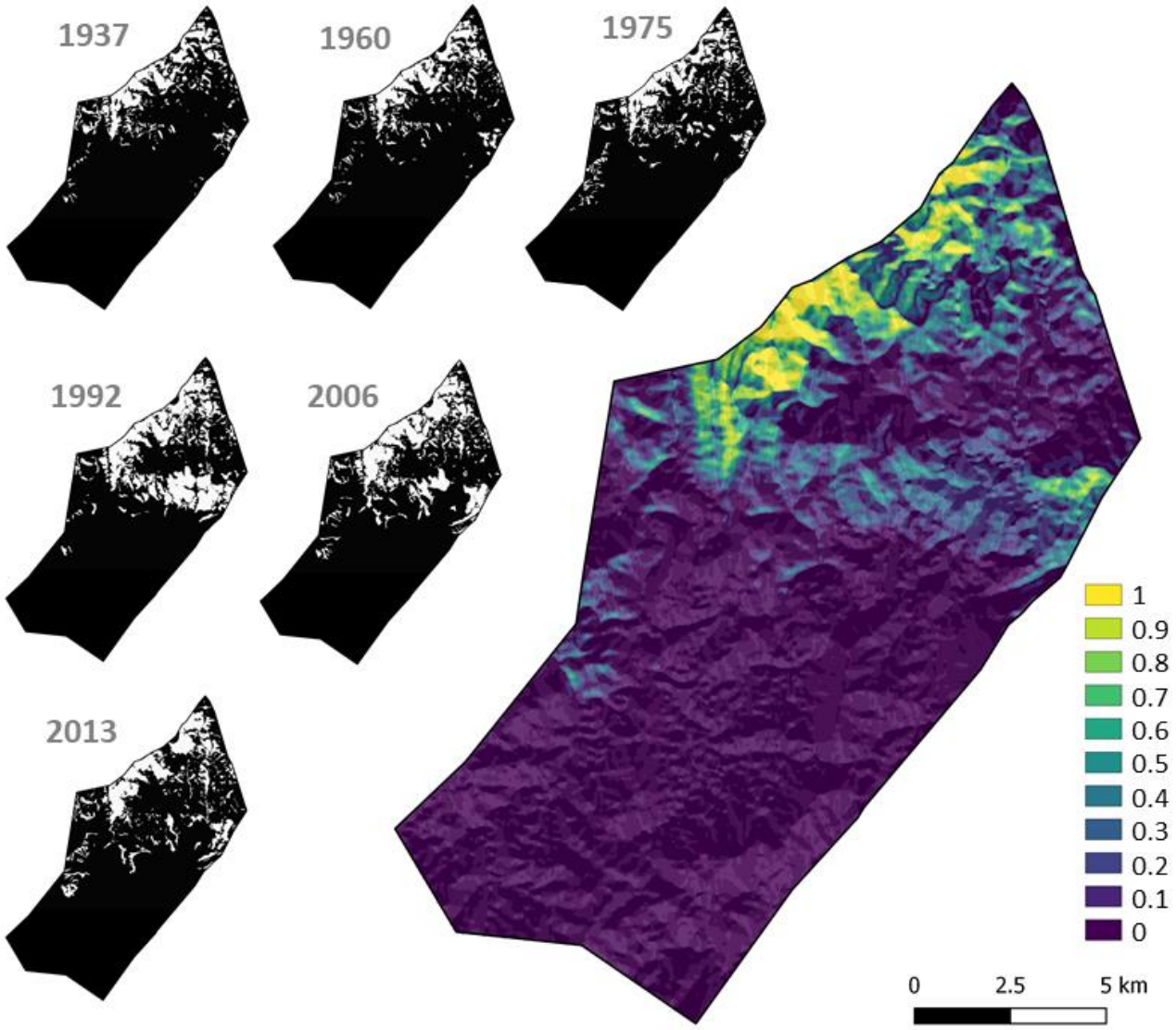


Figure 3.4. Maps of open and closed vegetation types (left) in Hluhluwe Game Reserve based on aerial photographs, and (right) the Habitat Suitability Index map for closed vegetation. Dark colours indicate areas unsuitable for closed canopy vegetation, lighter colours are more suitable. Grey text shows the year each vegetation map depicts.

Closed canopy vegetation was found mostly on South facing aspects (Figure 3.3). The relationships between closed canopy vegetation and topographic features was distinct for these different aspects too. South facing aspects reached approximately 50% coverage at 300m elevation, while North facing aspects only reach 50% at approximately 450m. This difference was most pronounced for Slope where North facing aspects showed no discernible

increase until the steepest slopes. From the relationships between the vegetation coverage data and topographic features, it is clear that closed canopies are spatially organised, preferring south facing, steeply sloped, and concave landscapes (Figure 3.3). The HSI model confirmed the importance of the five topographic predictors, which were highly significant ($p < 0.01$) for all time periods. The resulting map shows good agreement with the aerial photograph maps as indicated by the Kappa index for the calibration ($K_{0.5} = 0.69 \pm 0.03$) and the validation ($K_{0.5} = 0.68 \pm 0.02$) datasets. I did not test for spatial autocorrelation as this was accounted for in the model, and the intention of the model was to specifically identify patterns in the landscape that result from spatial processes.

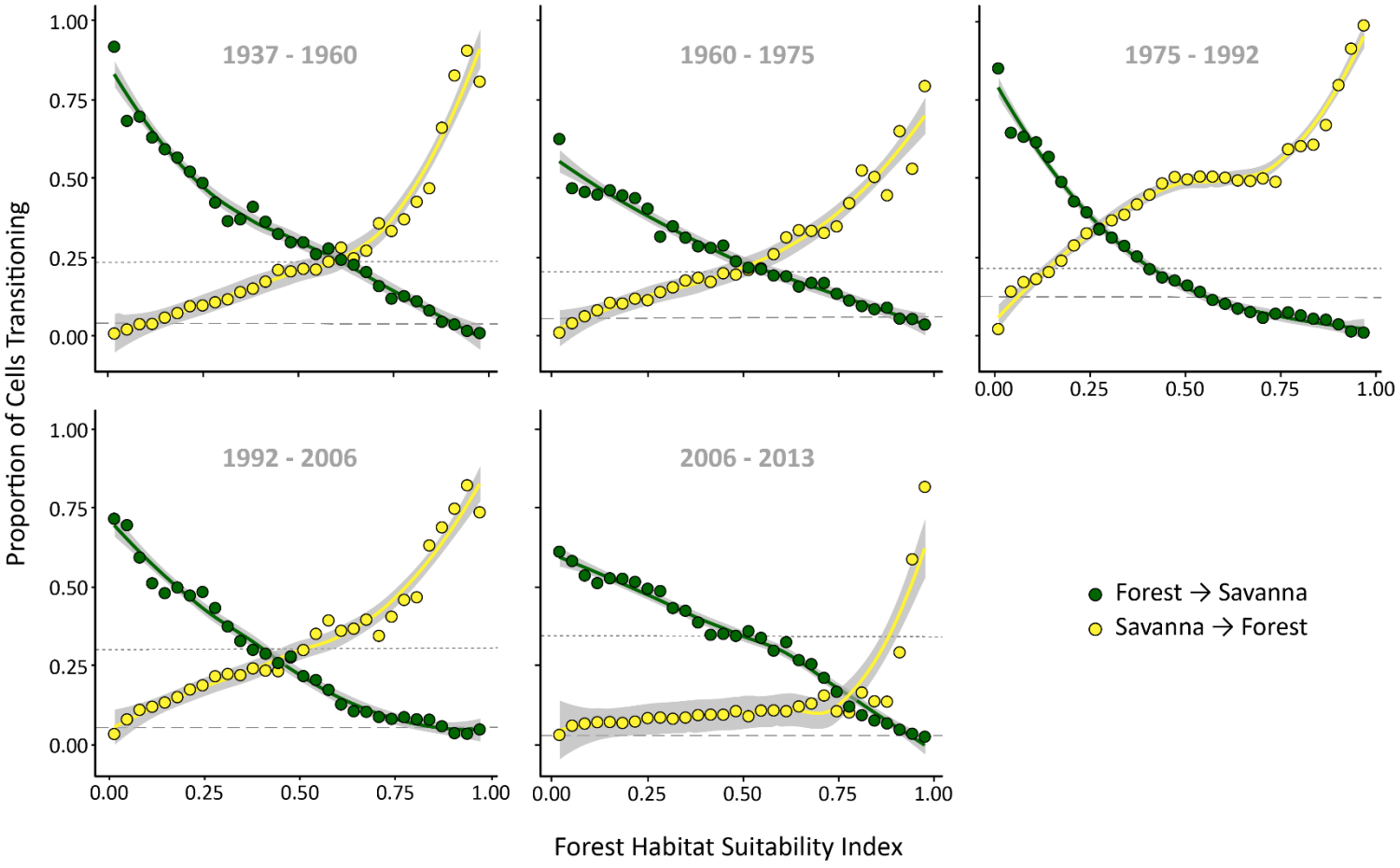


Figure 3.5. Relationships between the proportion of transitioning cells and the predicted Habitat Suitability Index values for each time period. Dotted and dashed lines show the null hypothesis where the proportion of forest to savanna and savanna to forest transitioning cells, respectively, are homogenous across the landscape and independent of the Habitat Suitability Index. Yellow and Green lines display a loess smoothing of data points.

The transitioning of savanna to forest and forest to savanna vegetation was not homogenous across the habitat suitability classes (Figure 3.5). Cells that were savanna were much more likely to transition to forest if they were in an area more suitable for forest and vice versa for forest cells in areas that were less suitable, this relationship held for both periods of increase and decrease. The transition probabilities in the 1975 to 1992 time period show a substantially greater number of cells transitioning from savanna to forest in areas of moderate suitability compared to the other time periods. The same is true for forest to savanna transitions occuring between 2006 and 2013. These two periods are associated with, respectively, the greatest increase and decrease in forest cover. The large changes in forest extent transpire not in the areas that are most or least suitable for forest, but in areas of moderate suitability where neither vegetation type has a firm hold.

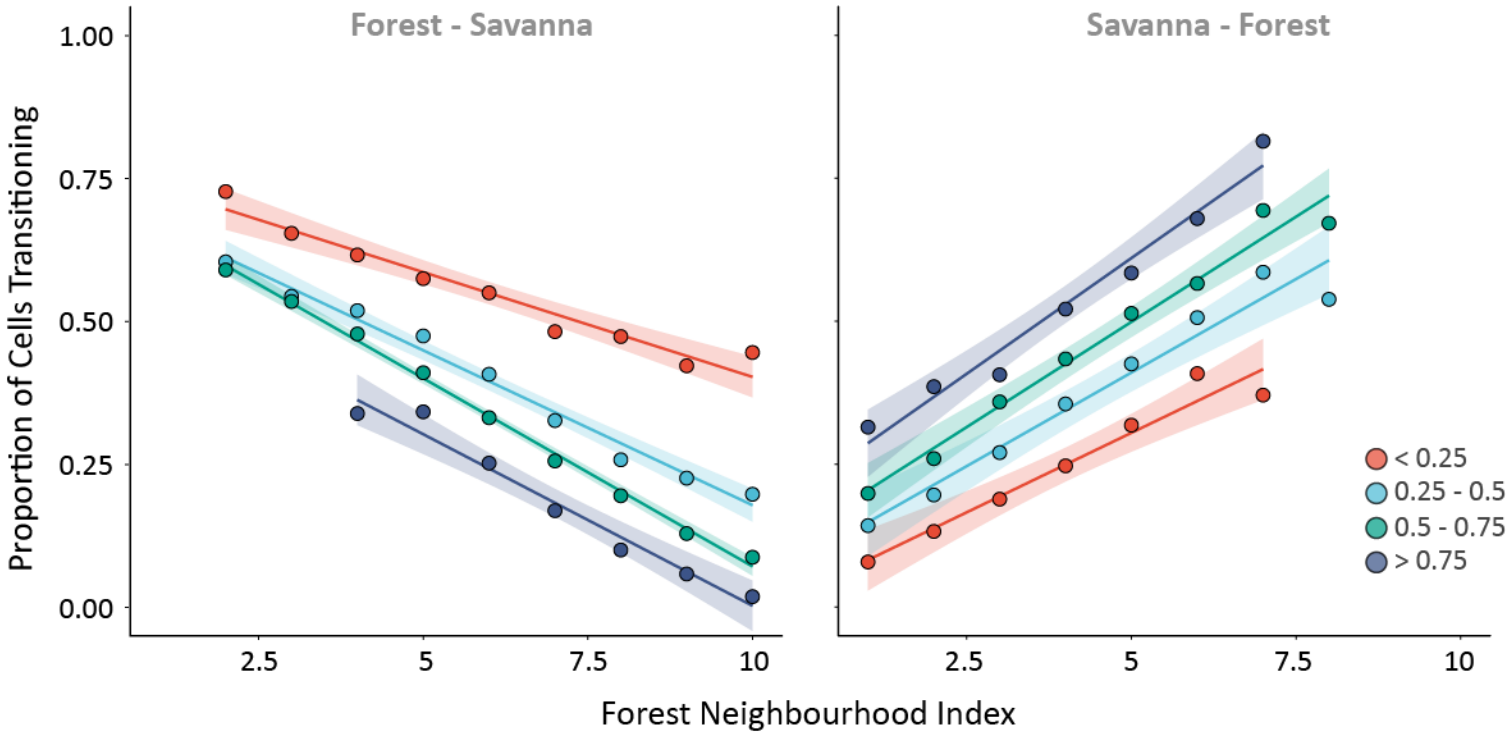


Figure 3.6. Relationship bewteen the proportion of cells transitioning and the neighbourhood of those cells, within four classes of Habitat Suitability. From least suitable (<0.25 HSI, red), through to most suitable (>0.75 HSI, dark blue). Low Neighbourhood Index values denote open environments with fewer forest neighbours, while high values denote closed environments with fewer savanna neighbours. The neighbourhood index is derived from cells within a 60 meter radius from the focal cell.

Fires in these systems start in savannas and are, usually, bound in extent by the presence of a grass fuel layer. Therefore, the protection from fire provided by the lack of grassy flammable fuels within the vicinity may supersede that of topographic features for large forest patches. This is evident in Figure 3.6 where the fuel characteristics (vegetation type) of the neighbouring cells are shown to be important in the proportion of cells transitioning between time periods. In areas of low habitat suitability, forest cells that are surrounded by other forest cells are 20% less likely to transition to savanna than those that have no forest neighbours.

These results show that forest cover increased since 1937, however this has not been a linear increase with a peak in extent in the early 1990's. The habitat suitability index, using topographic predictors associated with fire behaviour, relates to the expansion and contraction of forest vegetation (safety first). The expansion and contraction dynamics are however more nuanced, with the *in situ* vegetation neighbourhood playing a large role (teamwork).

3.5. Discussion

Expansion and contraction processes for closed canopy vegetation in Hluhluwe iMfolozi Park, between 1937 and 2013, are related to topographic features and neighbourhood dynamics. Given that 1) this is a protected area with no wood harvesting during the study period, 2) these topographic features are related to fire behaviour, 3) this area receives intermediate rainfall (~1000mm per annum), 4) there are limited effects of edaphic drivers (Gray and Bond, 2015) and 5) there is evidence of ancient grasslands beneath current closed canopy vegetation (West *et al*, 2001; Gillson, 2015), it is highly likely these vegetation types represent alternative stable states and the expansion and contraction processes are driven by fire. This supports similar work done by Ibanez *et al* (2013) in New Caledonia and Brook and Bowman (2006) in Australia, and Wood *et al* (2011) in Tasmania. During the study period there has been a net increase in closed canopy extent, although this oversimplifies the actual trajectory.

Closed canopy extent was at its peak in the 1992 aerial photograph. Bush encroachment is happening across Africa and the globe (Stevens *et al*, 2017). This has been attributed to changes in land use, altered grazing and fire regimes and also global drivers (O'Connor et al. 2014). This has been an issue in HiP from as early as the 1980's noted by Watson and MacDonald (1983) and Whateley and Porter (1983). Wigley et al (2009) noted an increase in tree cover in HiP as well as neighbouring commercial and communal lands from 1937 to 2006 and attributed this to global drivers such as increased atmospheric CO_2 and nitrogen deposition. The increase in woody biomass in savannas can be managed; Winston Trollope (1984) demonstrated the use of high intensity fires in topkilling trees and promoting a more open habitat, which has been used with some success in HiP (Balfour and Midgley, 2008).

Forest encroachment on the other hand, is a more serious threat to open ecosystems as the invasion of forest and thicket trees reduces the grass layer and results in a biome switch (Parr *et al*, 2012, Gordijn *et al*, 2012). Large portions of the more mesic parts of HiP were colonised by thicket vegetation from 1937 to 1992. This is especially evident between 1975 and 1992 (see Appendix Figure S2.2). During this period there were management interventions in the fire regime aimed at dealing with the woody thickening of savannas, particularly by species such as *Dichrostachys cinerea var. nyassana*, *Acacia karroo,* and *Acacia caffra*. By promoting early season burns, the aim was to topkill these species when the root reserves are depleted.

This, however, led to a change in the intensity and severity of fires, potentially altering the natural direction fires would burn and the distribution of fire refugia.

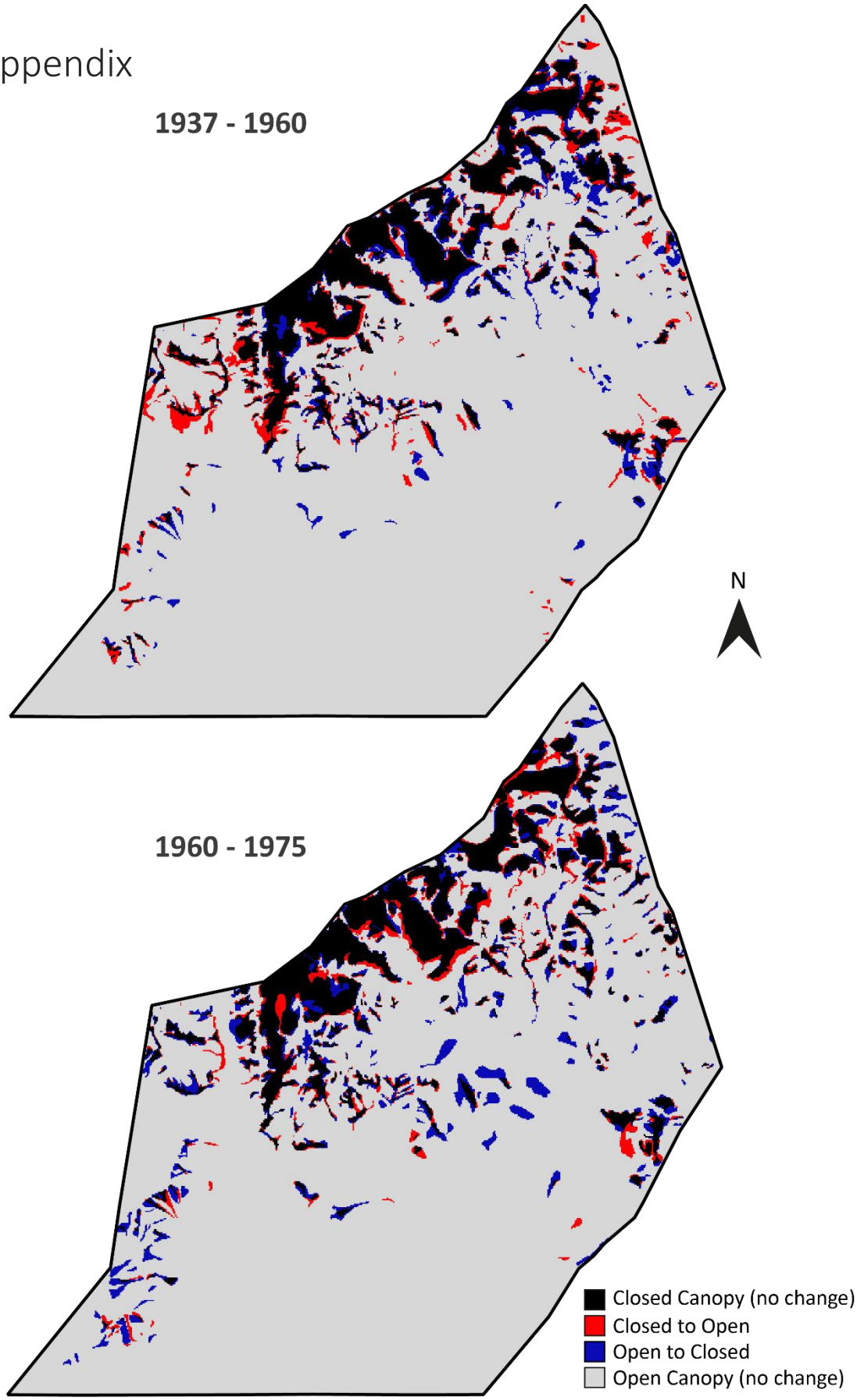
Closed canopies dominated areas identified by the HSI as suitable, and forests expanded and retreated along a gradient of habitat suitability. A low value of HSI, however, does not preclude the possibility of forest. From 1937 to 1975, expansion and contraction of closed canopy vegetation was restricted to the edges of closed canopy patches. Thus, the neighbourhood also determines the exposure to fire and the suitability of an area for a closed canopy. Small incursions of fire at the edge of a forest or thicket serve to sharpen the boundary, and rarely cause the damage witnessed after the firestorms. The severity of these firestorms is evident in the loss of large tracts of previously closed patches (see Appendix Figure S3.3). During these extreme fire events, it was possible for the fires to cross the savanna/forest boundary and continue to spread, causing widespread damage in the interior of these fire sensitive patches.

These extreme events, firestorms, burnt into both thicket and forest patches. While in the thickets we have observed the recovery of trees through basal resprouting, in the burnt forests we have seen a complete species turnover. Tree mortality following fires is much greater in forests than in savannas and thickets, despite similarities in the bark thickness of tree trunks. Forest trees do not seem to reach the 'fire-resistance threshold' proposed by Hoffmann et al (2012); instead the emphasis in these forests is on reaching the 'fire-suppression threshold' where canopy shading excludes flammable grasses. Following a firestorm, forests recover from a seed bank; pioneers are not nucleated and mature individuals are not found in the vicinity (Pammenter *et al*, 1985). There is a successional sequence where rapid growing pioneer forest species (i.e. *Trema orientalis, Croton sylvaticus, Celtis africana*) establish and generate a microclimate/environment suitable for later successional forest species (e.g. *Englerophytum natalense*) to establish (See Chapter 5).

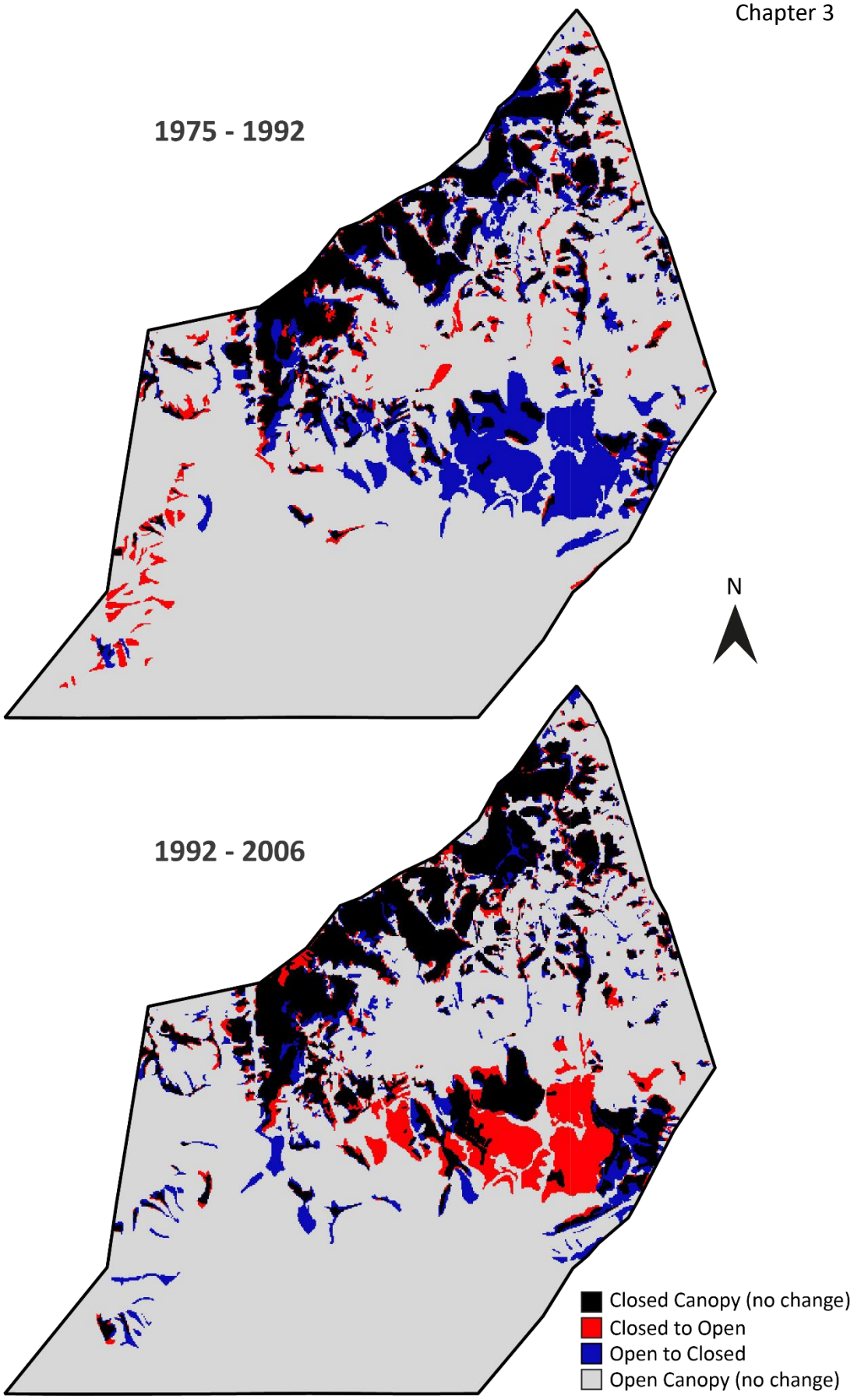
The application of a habitat suitability model to identify regions of low fire risk, or potential fire refugia, clearly has merit in HiP. Notwithstanding the overall increase in closed canopy extent over the study period, it is the recent trend of loss that is a cause for concern. Despite concerns over the spread of closed woody forest and thicket, it is important to note that a meagre 0.1% of South Africa, of a potential 7%, is covered by indigenous forest (Mucina and Rutherford, 2009). The Scarp Forest found in HiP has high levels of biodiversity (six endemic

genera and one endemic family of trees) and is severely underrepresented in protected areas. The trend of late (1992 onwards) is a decrease in closed canopy extent (Table 3.1) with sudden major losses (see Appendix Figure S3.3.), most likely associated with extreme events. The conditions necessary for a firestorm to develop are exceedingly rare. Over the period of 2001 to 2008, less than three days of 30' 30' 30' conditions occurred, with the longest consecutive record of 11 hours occurring on the day of the firestorm in 2008, the 15th September (Browne, unpublished thesis). The required amalgamation of these 30' 30' 30' conditions with sufficient fuel and an ignition event make firestorms difficult to predict and even harder to forecast into the future. Globally there is evidence for increasing lengths of fire seasons, greater variability in rainfall events and a likely increase in temperature extremes (Jolly *et al*, 2015). Does this mean the end for our forests as the advantageous effects of increased CO_2 for tree growth and forest encroachment are overridden by extreme fires?

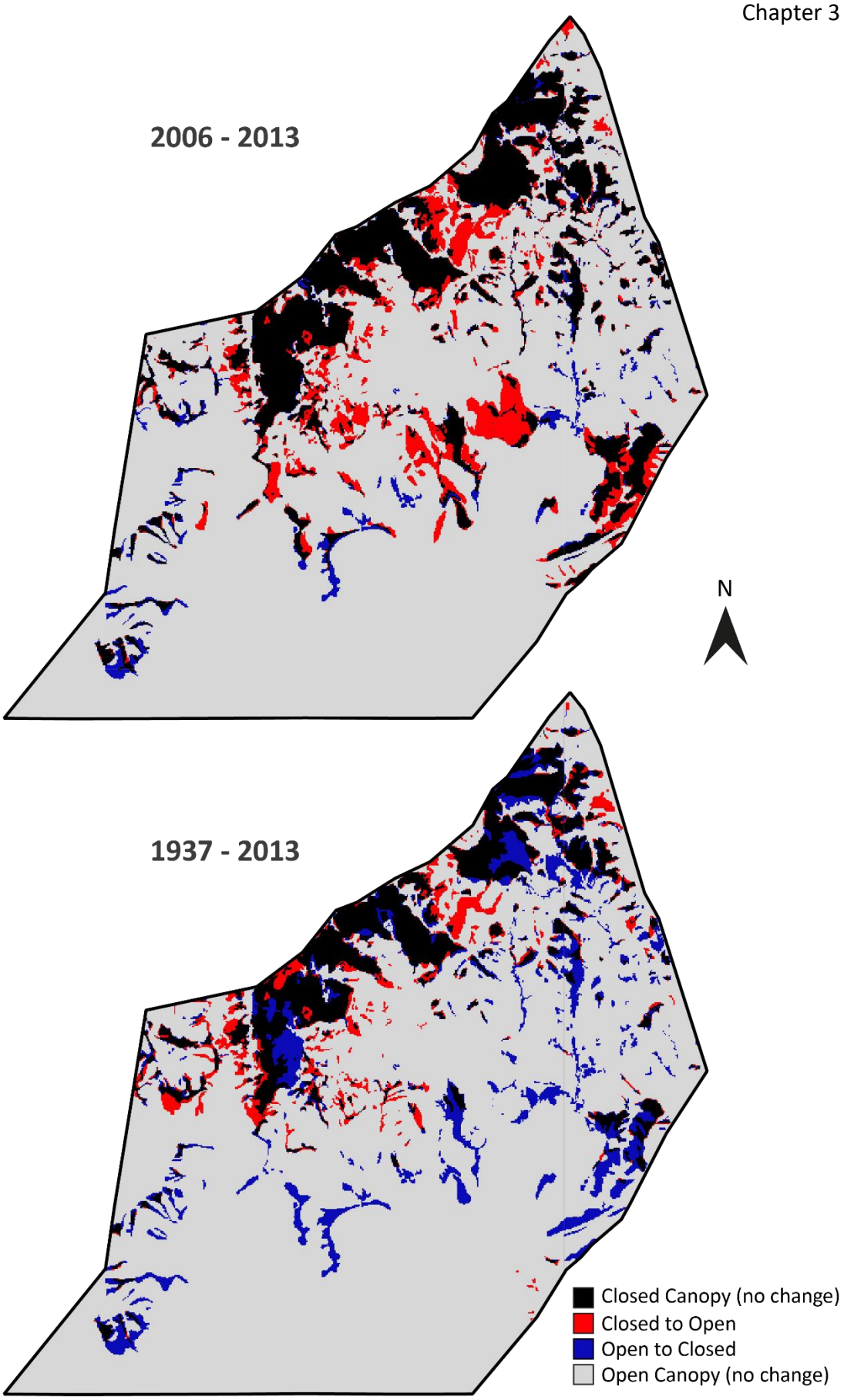
3.6. Appendix



Appendix Figure S3.1. Maps of vegetation change in northern HiP showing change from (top) 1937 to 1960, and (bottom) 1960 to 1975



Appendix Figure S3.2. Maps of vegetation change in northern HiP showing change from (top) 1975 to 1992, and (bottom) 1992 to 2006



Appendix Figure S3.3. Maps of vegetation change in northern HiP showing change from (top) 1975 to 1992, and (bottom) the entire study period from 1937 to 2013.

Chapter 4

Any way the wind blows

A mechanistic understanding of fire behaviour and forest persistence in a fire-prone landscape

4.1. Abstract

As opposed to widely available correlative approaches, a mechanistic understanding of fire spread and behaviour on complex terrain could advance our understanding of savanna-forest co-existence and provide insight into the presence and persistence of enigmatic forest patches in a fire-prone ecosystem. I used a fire spread model to predict fire behaviour (rate of spread) based on different wind directions and speeds in Hluhluwe Game Reserve at a 30m resolution on a homogeneous fuel layer to focus explicitly on the interaction between fire, topography and wind. Fire behaviour predictions were then compared to the earliest records of forest distributions, captured in aerial photographs in 1937. Wind direction used in the prediction of fire behaviour had a significant effect on the distribution of 'fire shadows'. Large portions of the landscape show lower rates of spread. When predictions are based on actual fire season conditions these areas are generally occupied by forests. The mechanism proposed here allowing for forest establishment is a local scale modification of fire regime creating pockets where fires are most likely to peter out resulting in patches with low fire return intervals. Fire sensitive forest species are able to establish in these areas, from which point a positive feedback loop reinforces the persistence of the forest. Prescribed fires are now burnt under safe conditions and the directionality of fires is seldom considered. Management should attempt to set prescribed fires under 'natural' burning conditions to prevent large losses of forest vegetation.

Keywords: fire behaviour, wind, forest, savanna, fire refugia, Alternative Stable States

4.2. Introduction

Traditionally global vegetation distribution is considered to be closely coupled to climatic conditions (Holdridge, 1947; Whittaker, 1975; Henderson-Sellers, 1994). Consequently a number of classification schemes were developed (most notably Holdridge, 1947 and Whittaker, 1975) which employ a bioclimatic envelope approach to predict global vegetation distributions (Henderson-Sellers, 1994). Whittaker (1975) outlined the difficulties in applying this approach and recognised a range of conditions for which this relationship does not hold.

Within this 'uncertain ecosystems' envelope there is the potential for a system to support grasslands, shrublands, woodlands or forests (Whittaker, 1975; Bond, 2005). Climatic factors, essentially, set the limit for potential plant growth; however the realized vegetation is a result of the interactions of a suite of biotic and abiotic drivers (Bond, 2005). Despite the narrow range of conditions encompassed by the 'uncertain ecosystem' envelope, it accounts for a substantial portion of the earth's terrestrial surface (Fig. 1. in Bond 2005). Of particular interest to this study is the savanna-forest mosaic where the climatic vegetation potential is not reached due, especially, to the effects of fire and herbivory and modified by soils (Whittaker, 1975; Bond, 2005; Sankaran et al, 2005).

The savanna biome is a dynamic biome defined by the presence of a continuous C4 grass layer interspersed with trees (Sankaran *et al*, 2005; Scholes and Archer, 1997). Sankaran *et al*. (2005, 2008) found that woody cover is largely limited by mean annual precipitation until a threshold of 650mm, above which disturbances and other regulatory variables are the main limitation to woody cover. These regulatory variables fall into two broad categories: "top-down" and "bottom-up" controls (Staver *et al*, 2009; Weltzin and Coughenour, 1990). Bottom-up controls encompass resource-limiting factors such as water availability, soil nutrients, and access to light (Weltzin and Coughenour, 1990), while top-down controls describe disturbance regimes such as fire and herbivory (Bond, 2008).

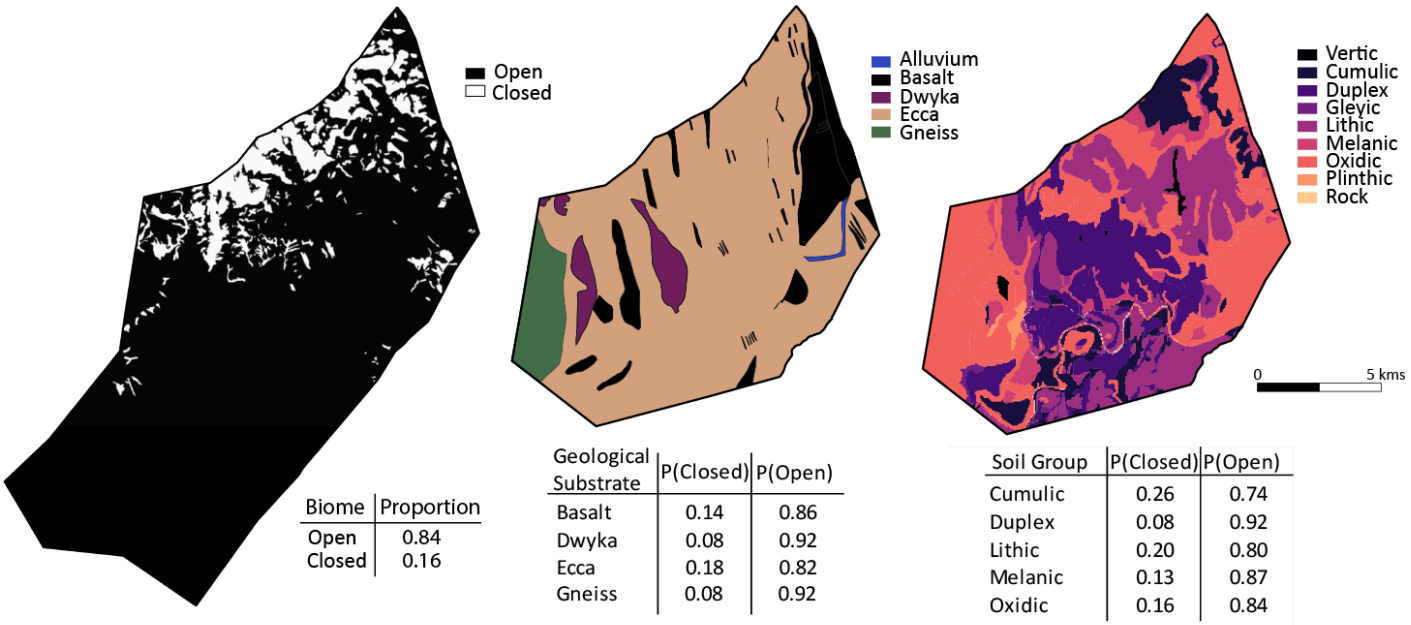
It is clear that while low rainfall limits maximum woody cover, rainfall alone fails to explain what limits woody plants in wetter regions that should support closed canopy forest. This issue is highlighted in regions where open grasslands and savannas occur in the presence of dense forests (Figure 4.1), creating landscape mosaics with abrupt boundaries between

vegetation types (Warman and Moles, 2009). Examples of these vegetation mosaics are found in Brazil (Hoffmann et al, 2009), Ghana (Markham and Babbedge, 1979; Swaine, 1992), the Central African Republic (Beauvais, 2009), Ivory Coast (Goetze et al, 2006; Hennenberg et al, 2006), India (Mariotti and Peterschmitt, 1994; Puyravaud et al, 1994), Madagascar (Virah-Sawmy, 2009), New Caledonia (Perry and Enright, 2002; Stevenson and Hope, 2005) and Australia (Bowman, 2009).

Figure 4.1. Aerial photographs of Northern Hluhluwe iMfolozi Park from 2013 showing the mosaic of open and closed canopy vegetation. Black lines indicate the park boundary. (See Appendix Figure S4.1 for the relationship between tree cover and rainfall in HiP).

Despite a growing acceptance of the idea that savannas and forests represent alternative stable states, there is strong criticism surrounding the methods used and interpretation of data (Veenendaal *et al*, 2014; Hanan *et al*, 2013). The underlying contention is between proponents of two main approaches to understanding forest-savanna distributions, the "bottom-up" approach (where forests are limited by abiotic factors such as soils and climate), versus the "top-down" approach (where forests are limited by consumers such as herbivores and fire) (Bowman, 2000). Examples of edaphic, climatic and fire limitation are discussed below.

Staver *et al* (2011) demonstrated that tree cover in Africa is limited by the amount and the seasonality of rainfall; they also highlighted the critical role of fire in the differentiation of high and low tree cover (i.e. forest and savanna, respectively) in areas receiving intermediate rainfall (from 1000 mm to 2500 mm per year). Fire limits woody cover by preventing tree recruitment, as saplings are continually stuck in what has been termed the "fire-trap" until they are afforded the opportunity to escape by growing into adult trees (Bell, 1984; Higgins et al, 2000; Bond and Midgley, 2001). It is widely accepted that positive feedback loops with fire can maintain forest and savanna patches in these mosaics (Geiger *et al*, 2011).



Biome	Proportion
Open	0.84
Closed	0.16

Geological Substrate	P(Closed)	P(Open)
Basalt	0.14	0.86
Dwyka	0.08	0.92
Ecca	0.18	0.82
Gneiss	0.08	0.92

Soil Group	P(Closed)	P(Open)
Cumulic	0.26	0.74
Duplex	0.08	0.92
Lithic	0.20	0.80
Melanic	0.13	0.87
Oxidic	0.16	0.84

Figure 4.2. Maps of Hluhluwe iMfolozi Park showing the distribution of Open and Closed biomes in 1937, geological substrates and soil groups with the proportion of biomes in each category displayed below. There was no significant difference between the overall proportion of open and closed vegetation and the proportion of open and closed vegetation types on different geological substrates ($X^2_{0.05,3}$= 0.105, p > 0.05) or soil groups ($X^2_{0.05,5}$= 0.135, p > 0.05).

Experimental exclusion of fires in mesic savannas is usually followed by an increase in woody biomass and an increase in forest species which is used as evidence for alternative stable states (Warman and Moles, 2009; Hoffmann *et al*, 2012; Murphy and Bowman, 2012). This is evident in the mesic savannas of Hluhluwe-iMfolozi Game Reserve in Kwa-Zulu Natal where

fire suppression and low intensity management burns have allowed tree invasion and thickening in savannas. Topographic characteristics of a landscape (e.g. slope, aspect, topographic position) play an important role in determining the distribution of vegetation and biodiversity because of their role as one of the key factors controlling the spread of fire. This was noticed a century ago by Aitken and Gale (1921) who, on a botanical survey to the area, noted: *"The trees grow closest together along the country lying just beneath the western mountain boundary and near the river. All the trees found in the open veld are found growing along the rivers, which form bases of colonization from which the trees migrate into the stretches of open country lying between the rivers; consequently the trees grow sparsely scattered in country midway between two rivers, and densely near each river."*

Lehmann *et al* (2011) presented a range of environmental conditions in which savannas occur; however they also state that "some proportion of the land is always not-savanna". Topography acts as a local scale modifier of fire behaviour. Geldenhuys (1994) suggested that the distribution of forests in fynbos landscapes in the Southern Cape region was determined by their position relative to the strong winds that drive extreme fires. Refugia within this 'firescape' occur where topography hampers fire spread, creating areas where the fire return interval is longer, the probability of burning is lower (Mermoz et al, 2005; Penman et al, 2007) and fire intensity and severity are lower (Kushla and Ripple, 1997; Alexander et al, 2006; Holden et al, 2009; Bradstock et al, 2010).

Effects of fire frequency on habitat structure are dependent on the spatial characteristics of fire, its size and severity (Whelan et al, 2002). Variation in fire size and severity, in turn, are largely dependent on three main factors, fire weather, fuels and topography (Catchpole, 2002; Bradstock et al, 2010). Whereas weather and fuel are not temporally and spatially static in the landscape, topography remains relatively fixed, so there is some degree of spatial regularity in the topographic effects on fire behaviour. Forests are restricted to higher altitudes in Hluhluwe where higher rainfall allows for their occurrence. It is within these higher altitudes where we see co-existence of forest and savanna. At a broad scale, elevation/rainfall predict the possibility of co-existence, at a fine scale, the actual pattern of forest distribution may be controlled by the topographic modifications of fire behaviour. Here we test the assumption that forest and savanna can coexist as ASS through topographic modifications of fire behaviour.

4.3. Materials and Methods

Study Area

Hluhluwe-iMfolozi Park (28°12'41"S 31°59'31"E), situated in Northern Kwa-Zulu Natal, South Africa, covers over 960 square kilometres of hilly countryside. The park has a coastally modified climate with much of the variability in local weather being related to topography (Ezemvelo KZN Wildlife, 2011). Mean annual precipitation is closely linked to altitude in the park (Balfour and Howison 2001), producing a rainfall gradient from ~1000 mm per annum in the Hluhluwe section (580m a.s.l), to ~600 mm per annum in the iMfolozi section (70m a.s.l). Annual rainfall is strongly seasonal with the majority falling during the warm summer months (October – March), whereas winter is characterized by cool, dry conditions punctuated by warm, dry conditions brought on by berg winds. Mean minimum and maximum temperatures in the Hluhluwe portion of the park are, respectively, 18 °C and 29 °C in summer (January) and 11 °C to 23 °C in winter (July) and are also strongly influenced by altitude. Thunderstorms are a common feature of the summer rainfall season and lightning strikes occur in densities of approximately five ground-flashes per square kilometre per year (Ezemvelo KZN Wildlife, 2011).

Fire Spread Model

A number of models exist for the prediction of fire behaviour, the most widely used of which is based on Rothermel (1972). I used the *Rothermel* package (Vacchiano and Ascoli, 2004) in R (R Core Team, 2013), which implements Rothermel's (1972) fire spread model, to predict fire behaviour, and especially rate of spread (ROS), in Hluhluwe Game Reserve at a 30m resolution. Meteorological data were acquired through the South African Weather Service archive for the nearest weather station, in the Bushlands district (-28.13938 S, 32.3949 E), approximately 20km from the study area, for the years 2001 to 2010. Using hourly wind speed (m/s) and wind direction (°) data I calculated averaged monthly wind direction and speed for daylight hours, the time during which most fires burnt.

I selected a homogenous fuel layer over the entire study area. This removes the effects of different fuel types and focuses explicitly on the interaction between fire, topography and wind. The fuel model used was based on data collected by Wills (1987) in Hluhluwe Game

Reserve, parameters for which are show in Table 4.1. For the topographic variables required, I used the 30m resolution ASTER GDEM, and calculated slope and aspect from this using the *raster* package in R. A slope layer was calculated for each wind direction, giving a directional slope (positive and negative values indicate an upslope and downslope respectively).

Table 4.1. *Acacia nilotica* Savanna fuel model parameters (Wills, 1987)

Fuel Loads	
Fine Dead Fuel (1 hour timelag)	312 gm^{-2}
Medium Dead Fuel (10 hour timelag)	2 gm^{-2}
Live Herbaceous Fuel	61 gm^{-2}
Live Woody Fuel	4 gm^{-2}
Surface Area to Volume Ratios	
Fine Dead Fuel (1 hour timelag)	66 $cm^{-2}cm^{-3}$
Medium Dead Fuel (10 hour timelag)	3.6 $cm^{-2}cm^{-3}$
Live Herbaceous Fuel	59 $cm^{-2}cm^{-3}$
Live Woody Fuel	59 $cm^{-2}cm^{-3}$
Heat Content	19500 kJ/kg
Fuel Bed Depth	0.44 m
Moisture of Extinction	20 %

The implementation of Rothermel's (1972) fire spread model in the *Rothermel* package in R does not allow for a negative slope angle (i.e. downslope fires). Slope is known to modify ROS, with an increase in slope leading to much higher rates of spread (Luke and Mcarthur, 1978; Trollope, 1984). To predict ROS on negative slopes, I used Cheney's (1981) equation:

$$R = R_0 \exp(\propto \theta_s)$$

R = Rate of Spread ($m.s^{-1}$)

R_0 = Rate of spread on level ground ($m.s^{-1}$)

α = 0.0693 (A constant)

θ_s = Slope angle (°)

Basic fire behaviour predictions were calculated for a range of different wind directions (Figure 4.3). 360 maps of rate of spread were calculated for each 1° wind direction interval. I then created four separate maps of rate of spread for each cardinal direction by averaging the 5 maps on either side of each cardinal direction. Wind speed was kept constant at 10km/hour. The *Rothermal* package in R allows for a static and a dynamic fuel moisture value in the fire spread model. I selected the static model, which does not allow for fuel curing and is constant across slopes and aspects, thus reducing the effects of solar radiation on ROS predictions. Fuel moisture values (4.5%, 5%, NA, 86%, 144%) for the fuel model are taken from Van Wilgen and Wills (1988).

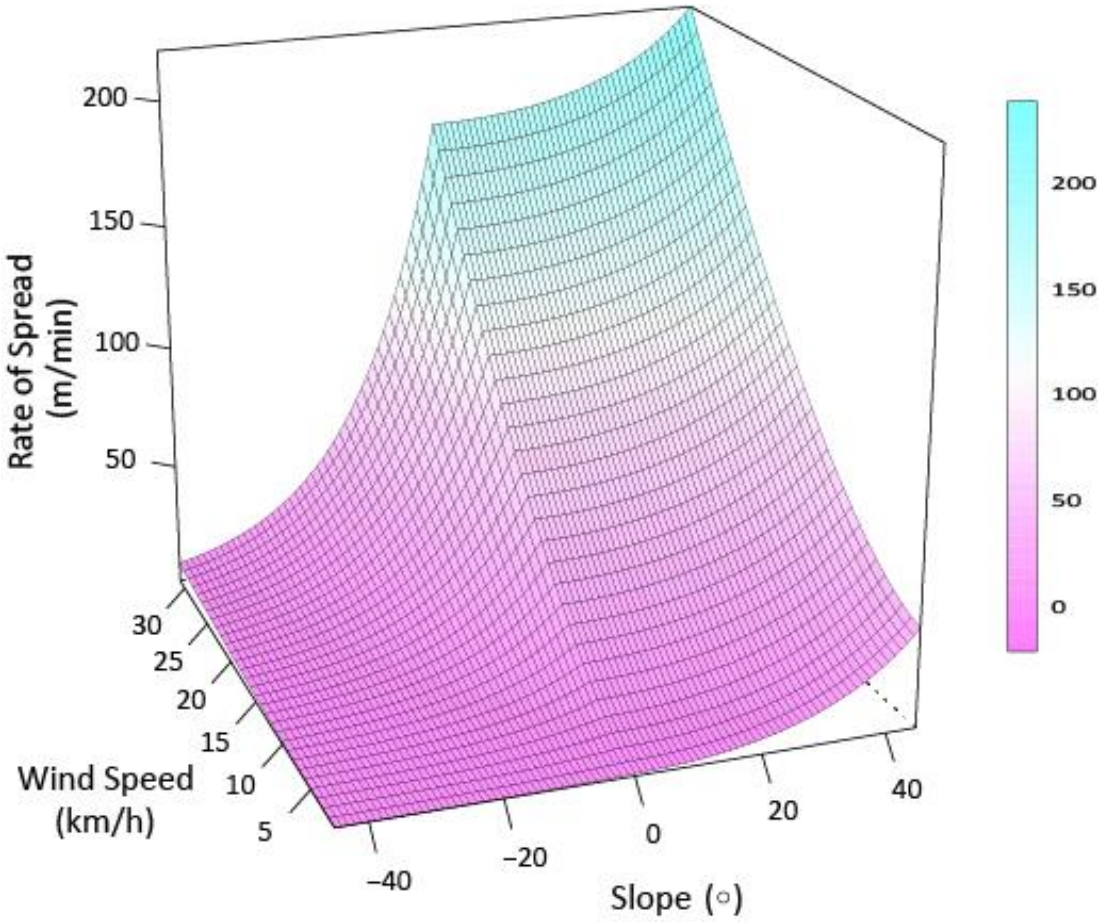


Figure 4.3. Surface showing the predicted effects of Slope and Wind Speed on Rate of Spread, based on Rothermel (1972). Values are calculated using the *Acacia nilotica* fuel model (Wills, 1987). Scale bar indicates the colours used to indicate Rate of Spread.

Forest Mapping

In order to map forest vegetation in Hluhluwe Game Reserve I produced maps of closed canopy vegetation from historical aerial photographs, obtained from the National Geo-spatial Information (NGI) office. I selected the earliest time period, 1937, for use in this study as this is likely to resemble the natural fire regime most closely, human populations within South Africa were small (<20% of their current number) and their impacts on vegetation would have been the lightest over the study period. The 1937 aerial photographs were scanned and resampled to a pixel resolution of $1m^2$, and then mosaicked and geo-referenced using high quality ortho-rectified aerial photos from 2013 using QGIS Pisa. The average horizontal root mean square errors was less than 15m and the average root mean square error was 7.25m.

A grid, with cells 10m x 10m, was draped over the mosaicked images and each cell was manually classified as either closed canopy vegetation (F) or open vegetation (S) with a value of 1 and 0 respectively. For cells that contained both vegetation types, those with more than 50% tree cover were classified as closed canopy. The classifications were visually compared to vegetation maps of HiP by Henkel (1937). The spatial resolution of the classified images was degraded to 30m x 30m to match that of the ASTER Global Digital Elevation Model (DEM).

Predicting forest from different winds

I modelled the probability of forest occurrence in classes of the ROS, based on the actual distributions of forest in the 1937 aerial photographs and the predominant wind direction during the fire season. Two separate models were built, one with Elevation/Rainfall, and one without. The models were constructed using a Generalised Linear Model (GLM), which is particularly well suited to species distribution modelling of presence-absence data (Guisan, 2002; Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). I then applied the model to the ROS Index maps for different wind directions to show the expected pattern of forest distribution based on each direction.

4.4. Results

The dominant winds during the fire season are Northerly to North-Easterly winds with a median wind speed of approximately 2.3 $m.s^{-1}$ (Fig. 4). These are katabatic winds, also known as berg winds, which originate in the centre of South Africa on the plateau, and warm adiabatically as they descend the escarpment. Southerly winds during the fire season are associated with higher humidity and rarely coincide with fires (Archibald *et al*, 2017).

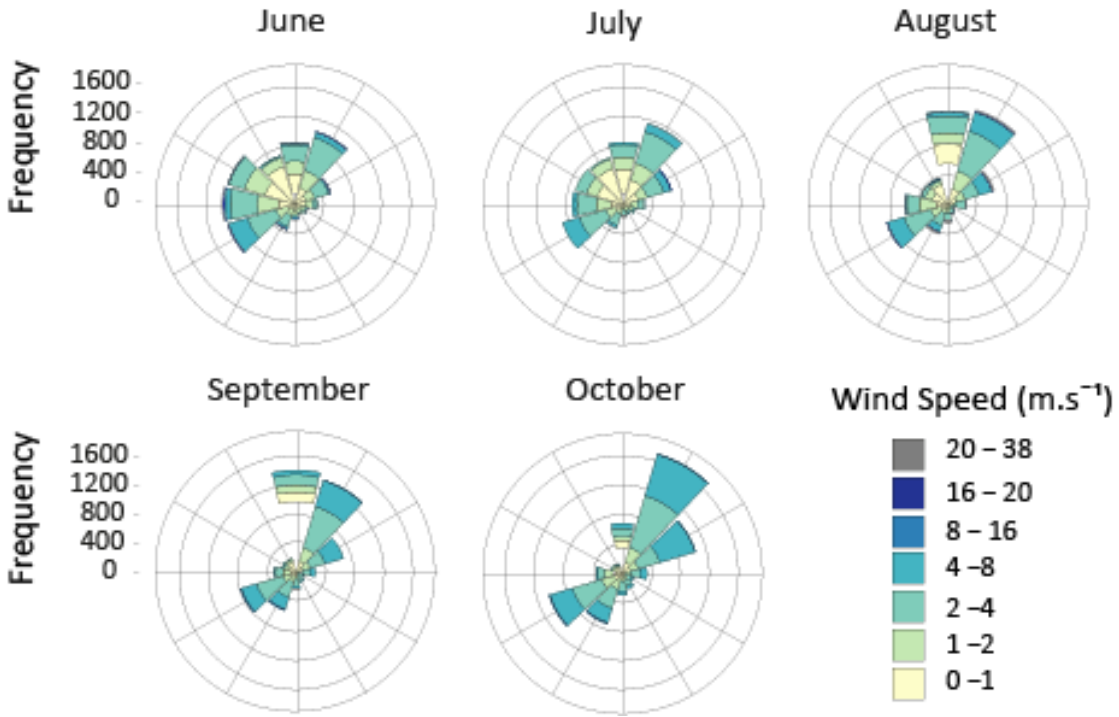


Figure 4.4. Wind Rose diagrams for each month during the fire season from a nearby weather station (Bushlands) from 2001 to 2010.

The wind direction used in the prediction of fire behaviour had a significant effect on the distribution of 'fire shadows' in Hluhluwe (Figure 4.5). Large portions of the landscape show lower rates of spread, while the areas of high rates of spread are generally less common. Rate of spread on flat ground is constant among the different wind directions. Focusing on the distributions of 'hampered spread' (blue) and 'enhanced spread' (red) in Figure 4.5 shows the effect of wind direction. The Rothermel model used to predict fire behaviour was static meaning that it did not allow for conditioning of fuels. North facing aspects are exposed to higher levels of solar radiation and hence evapotranspiration, meaning fuels would cure quicker and more completely than South facing aspects. Including aspect effects on fuel moisture in the model would exacerbate the differences in the Northerly wind predictions.

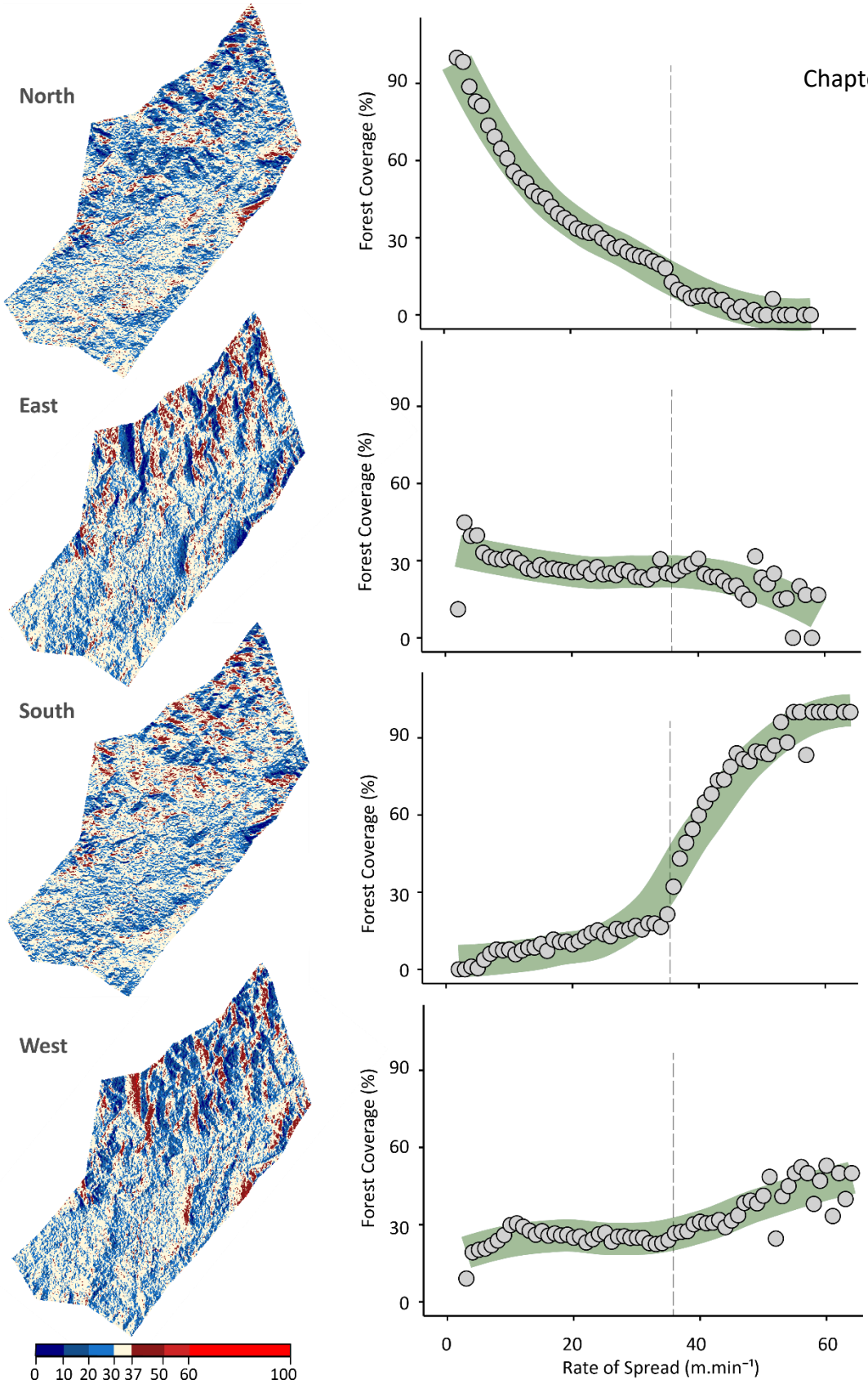


Figure 4.5. Rate of Spread Maps of Hluhluwe Game Reserve (left) based on the Rothermel fire equation for different wind directions (grey text). ROS values, from blue (low) to red (high) are in meters per minutes, based on a wind speed of 2.7 $m.s^{-1}$ (10 $km.h^{-1}$). I used a value of 2.7 $m.s^{-1}$ instead of the mean (2.3 $m.s^{-1}$) as the results are more intuitive when expressed in $km.h^{-1}$. Scatterplots (right) show the percentage of land within each ROS class that was covered by forest in 1937. Dotted lines indicate the rate of spread on flat ground.

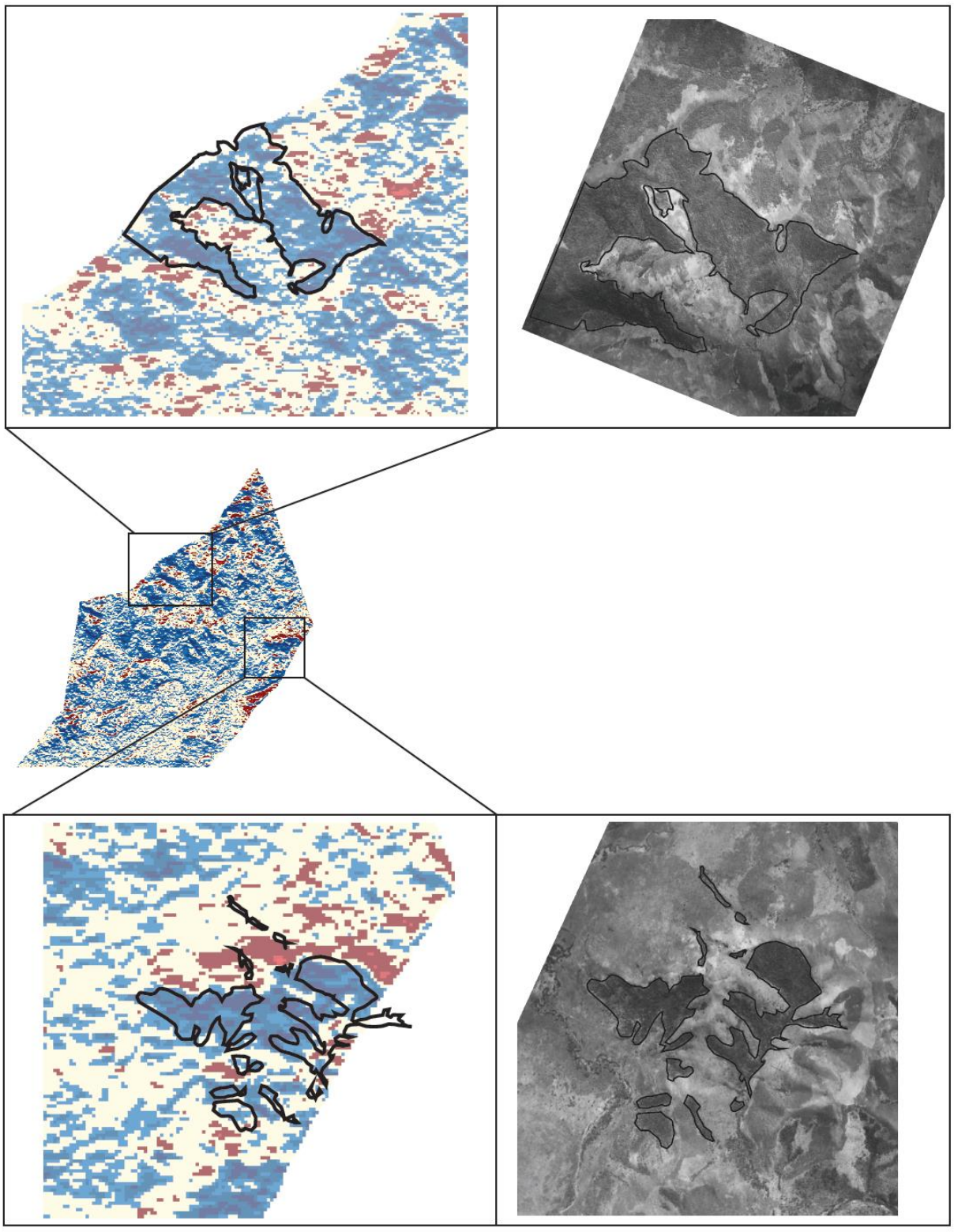


Figure 4.6. A comparison of predicted rates of spread for northerly wind direction (left) and aerial photographs (right) showing forest distributions in 1937. Inset (centre) shows the location of the photographs within the park. Rate of spread maps use the same colour scheme as Figure 4.5.

The relationship between Rate of Spread and observed forest extent was strongest for North and South winds (Figure 4.5). This is confirmed by the trends in cover on either side of the ROS on flat ground where East and West winds showed no noticeable change. The relationship for North wind ROS and forest coverage shows a steep logistic decrease in cover up to the flat ground spread rate (dotted line), a nick point in the relationship at this point and very little cover at higher rates of spread. There are still forests occurring in areas of high rates of spread, however this is most likely within the centre of a forest and so the neighbourhood dynamics override the fire behaviour (See Chapter 3).

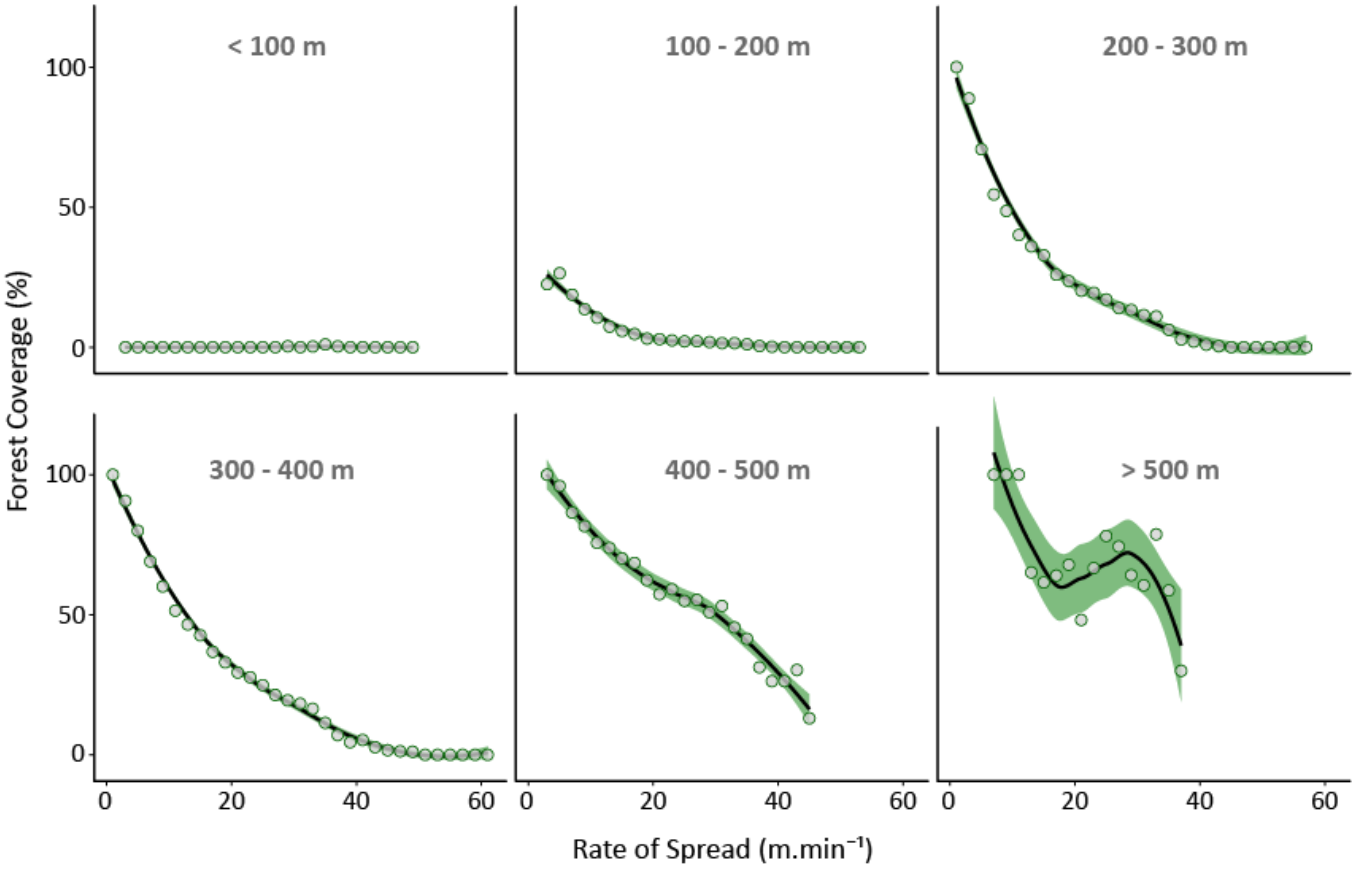


Figure 4.7. Percentage of land covered by forest in 1937 in relation to predicted rates of spread at different elevations. Elevations (meters a.s.l) are shown in grey text. Black lines display a loess smooth of data points. Wind direction (North) based on the dominant wind direction during the fire season.

Elevation, as a proxy for rainfall, has a significant effect on forest distributions with the majority of the forests occurring at higher elevations. The effect of ROS on forest distributions is modulated by the rainfall the area receives (i.e. there needs to be enough rainfall for forests to establish before ROS takes effect) (Figure 4.7). Elevation/rainfall predicts the possibility of

forests at a landscape scale, whereas at a fine scale, the pattern of forest distribution is more heavily impacted by fire behaviour. At lower elevations forests are restricted to the areas of lowest rate of spread but at higher elevations they can be found in areas of higher rates of spread. For example, for a given ROS value of 20m/min, the probability of forest is <0.05 at low elevations (100 – 200m) and 0.6 at higher altitudes (400 – 500m).

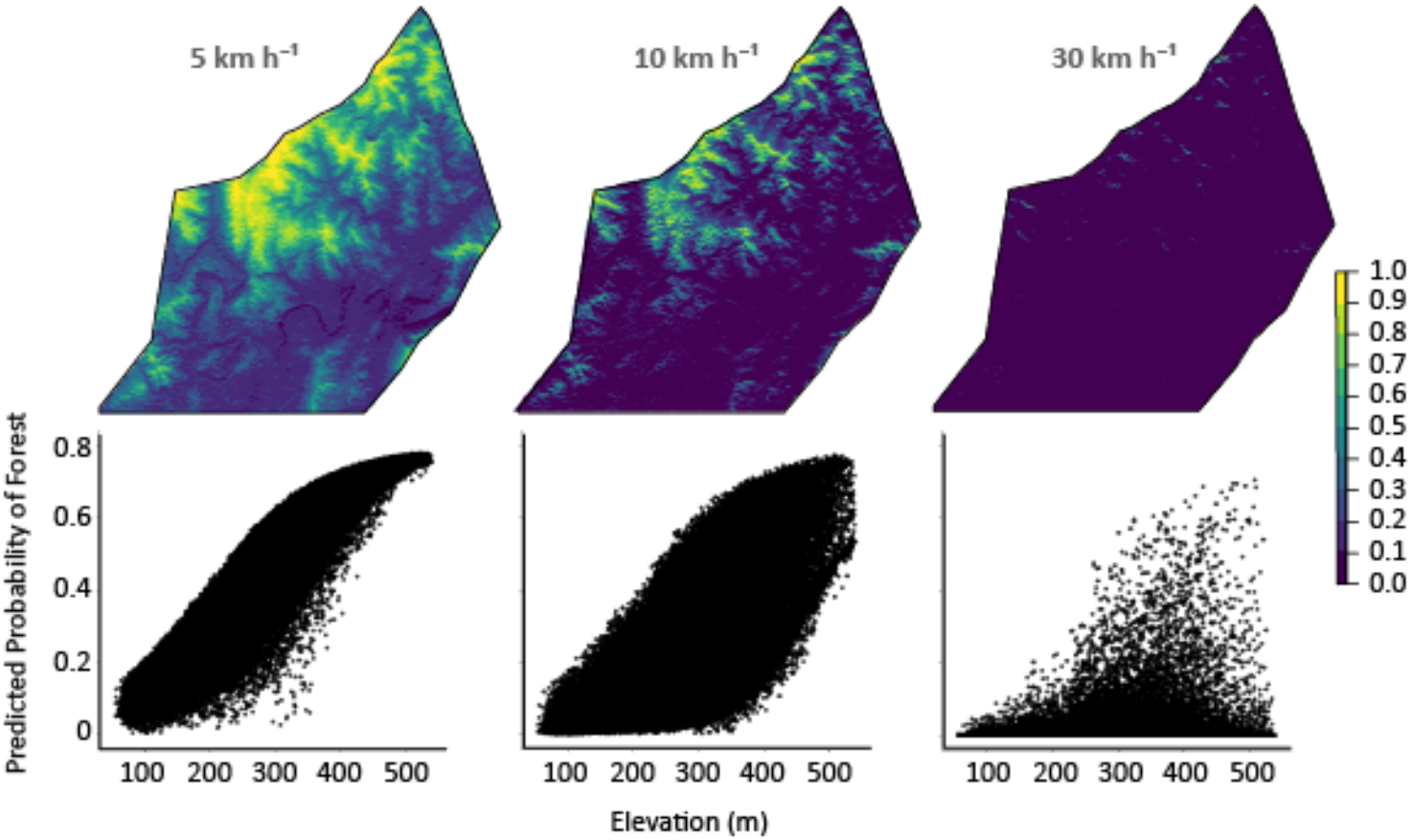


Figure 4.8. Modelled relationship between ROS and the probability of forest for three different wind speeds (grey text) displayed as maps (top) and the relationship between predicted forest and elevation (bottom). Scale bar displays the colours for predicted probabilities of forests on the maps. Points in the scatterplots are individual 30 x 30m cells.

Using the model predictions of fire refugia for forest distributions for a 10km/h Northerly wind, I simulated the distribution of forests based on 5km/h and 30km/h winds (Figure 4.8). Fire shadows with similar characteristics to those of the 10km/h predictions are widespread for the lower wind speed while for the 30km/h wind fire shadows are nearly eliminated with just a small number of miniscule patches (Figure 4.8). Relationships between tree cover and elevation (as a proxy for rainfall) display the effects of burning under mild and more extreme conditions, which resemble the relationship between tree cover in 2000 derived from remotely sensed data (Hansen *et al*, 2013) and rainfall (See Appendix Figure S4.1)

4.5. Discussion

Landscape scale patterns of forest distributions in Southern Africa have long been considered as anthropogenic in origin (Phillips, 1931; Phillips, 1963; Granger, 1984; Acocks, 1953; Feely, 1980) or related to edaphic limitation (Rutherford and Westfall, 1986; Mills *et al*, 2013). Geldenhuys (1994) suggested these patterns were more likely to be controlled by the interactions of topography, berg winds and fires in the Western Cape, South Africa. I was able to test this hypothesis by predicting fire behaviour for Hluhluwe iMfolozi Park using a homogenous fuel layer. This allows us to identify possible locations where forests first established in these open environments by removing the effects of solar radiation on evapotranspiration and species composition, and isolating the effects of topography and wind alone on fire spread. The mechanism proposed here allowing for forest establishment is a local scale modification of fire regime creating pockets where fires are most likely to peter out resulting in patches with low fire return intervals. Fire sensitive forest species are able to establish in these areas, from which point a feedback loop (Wood and Bowman, 2012) reinforces the persistence of the forest.

Though this study supports the importance of fire in shaping forest distributions, it does not necessarily exclude other explanations. For example, slope and aspect differences would also affect soil moisture and therefore the growth of forest trees. However, the importance of site factors operating through growth and survival of forest trees seems unlikely. The edaphic limitation hypothesis proposes that although the climate may be suitable for forest, edaphic constraints (soil types, drainage, nutrients and fertility) prevent the formation of forests in these mosaics (Bowman, 2000). In Australia, for example, soil phosphorus has long been thought to determine the boundary between 'rainforests' (closed forest) and sclerophyll (eucalypt-dominated) open woodlands (Beadle, 1958; Bowman, 2000). So, forests should occur where there are sufficient nutrients, and are limited by low nutrients, which allow for the presence of grasslands and savannas.

Figure 4.2 shows the array of soil groups supporting forests in 1937; soil types, and parent material are not closely correlated with the distribution of forests in Hluhluwe iMfolozi Park. This is supported by Gray and Bond (2013) who found no significant differences between soil nutrients of thicket, forest and savanna vegetation types and in all cases there were more

than sufficient nutrients to support the construction of forest biomass. Soil nutrient differences are likely a consequence, not a cause of different vegetation types according to these authors (Gray and Bond, 2013).

A major problem for site factors rigidly determining forest/savanna mosaics is that the components of the mosaic have not been stable over time. The configuration of closed canopy vegetation in Hluhluwe iMfolozi Park has vacillated since the first aerial photograph survey in 1937 to the most recent in 2013 (See Chapter 3). If vegetation distributions are driven by soils we would expect them to be more stable over time with forests unable to encroach onto 'nutrient poor' or physically unsuitable 'savanna' soils. Isotope studies reveal that most of the area that is forest was a grassland in the past switching to forest within the last couple of millennia (West et al. 2001; Gillson 2015). Thus the soil hypothesis for forests on forest soils and savannas on savanna soils is not supported in this study area.

Climate Envelope Models are based on the assumptions of Hutchinson (1957), where species distributions can be predicted using the range of climatic conditions in which a species occurs (Martinez-Meyer et al, 2004; Whittaker, 1975). Following this logic, forests should occur in all regions that can support forests climatically and non-forest vegetation in these areas are early successional or anthropogenic in origin. Patches of savanna and forest vegetation occur with boundaries of less than a meter in some cases between these strikingly different biomes. The idea that there is a climatic gradient across this distance sufficient to differentiate between biomes is not feasible.

Forest microclimates are vastly different to that of adjacent savannas with higher fuel moisture, reduced wind speeds (Biddulph and Kellman, 1998; Little et al., 2012; Ibanez et al, 2013) and little light reaching the ground layer (Hennenberg et al. 2006; Hoffmann et al. 2012; Charles-Dominique et al, 2018). However, carbon isotope ratios and palynological evidence shows ancient grasslands preceded current forest distributions, indicating that forests are secondary (West et al, 2000; Meadows and Linder, 1993, Gillson, 2015) and these open vegetation states are not anthropogenic in origin. The microclimate found in forests is concomitant with/subsequent to the establishment of forest, a feedback loop that reinforces presence but does not facilitate establishment. Within the higher rainfall regions of HiP thicket, forest, grassland and savanna vegetation types are all present (Figure 4.1). So while

the lower limit of forest distributions is controlled by rainfall, the coexistence of vegetation types is not explained by climatic drivers (Bowman, 2000).

Rainfall dictates the distribution range of forests at a larger scale than fire. Below ~ 400mm MAR, continuous fuel-beds are rare which restricts fire spread. Annual burnt area in Africa reaches a maximum at ~1000mm MAR, above which it is limited not by the biomass of grassy fuel, but by the extent of this fuel (savanna environments become rare above ~1200mm in Africa: Lehmann et al. 2011). It is within these more humid areas where the relationship is more nuanced, with fire behaviour and the prevailing wind direction (Geldenhuys, 1994), at a local scale, being important.

I did not consider temperature differences as constraints on forest distribution. However, evidence from Australia shows that forest seedlings are capable of germinating across a range of temperatures (Bowman, 2000, Stevens *et al*, 2014). Light and temperature may have an indirect effect on forest distributions through modifications of fuel characteristics, reducing fuel moisture on northern slopes but not southern slopes. This however, exacerbates, rather than negates, the effect of fire. The microclimate created by forests reinforces persistence, but appears to play little to no role in facilitating establishment.

There have been a number of changes in fire management policies since 1937. There is some debate as to whether or not these interventions had any noticeable effect on the season of fires and burned area (Archibald et al, 2012). Fire suppression and management during 1960's meant lower intensity fires were being burnt, also, from different directions, so fires may have burnt up to forest edges at a much higher speed. However, these fires were often set during days when fire danger was low, and so rate of spread and intensity would have been lower too. Fires burnt under safe conditions would have occurred under different wind directions and at lower wind speeds. The natural patterns of forest/savanna patch distribution would have been altered. The directionality of prescribed burns is seldom considered in the park but might significantly affect the boundary dynamics and therefore boundary locations of forest versus savanna. Also of concern is the sensitivity of forest distribution to higher wind speeds. As noted in Chapter 2, 'firestorms' have become common in the last couple of decades, so we need to know how quickly forest and thicket vegetation types can recover from these events if we're to predict the future of these biomes.

In silica simulations of fire present a number of problems. However, they provide us with a method of predicting the locations where fire will spread and also why the boundaries between vegetation types may be so sharp. There is not only lack of understory fuel in forests, but also conditions in the topographic template that hinder the spread of fires. Establishment of forests is most likely to happen in these areas, as the intensity of fires is lower and the return intervals are longer. Topographic fire refugia possibly increase the resilience of forests to regime shifts. However, fires that occur during extreme fire weather events are less likely to play by the rules, and higher wind speeds reduce the effectiveness of topographic refugia in protecting forests (Figure 4.8).

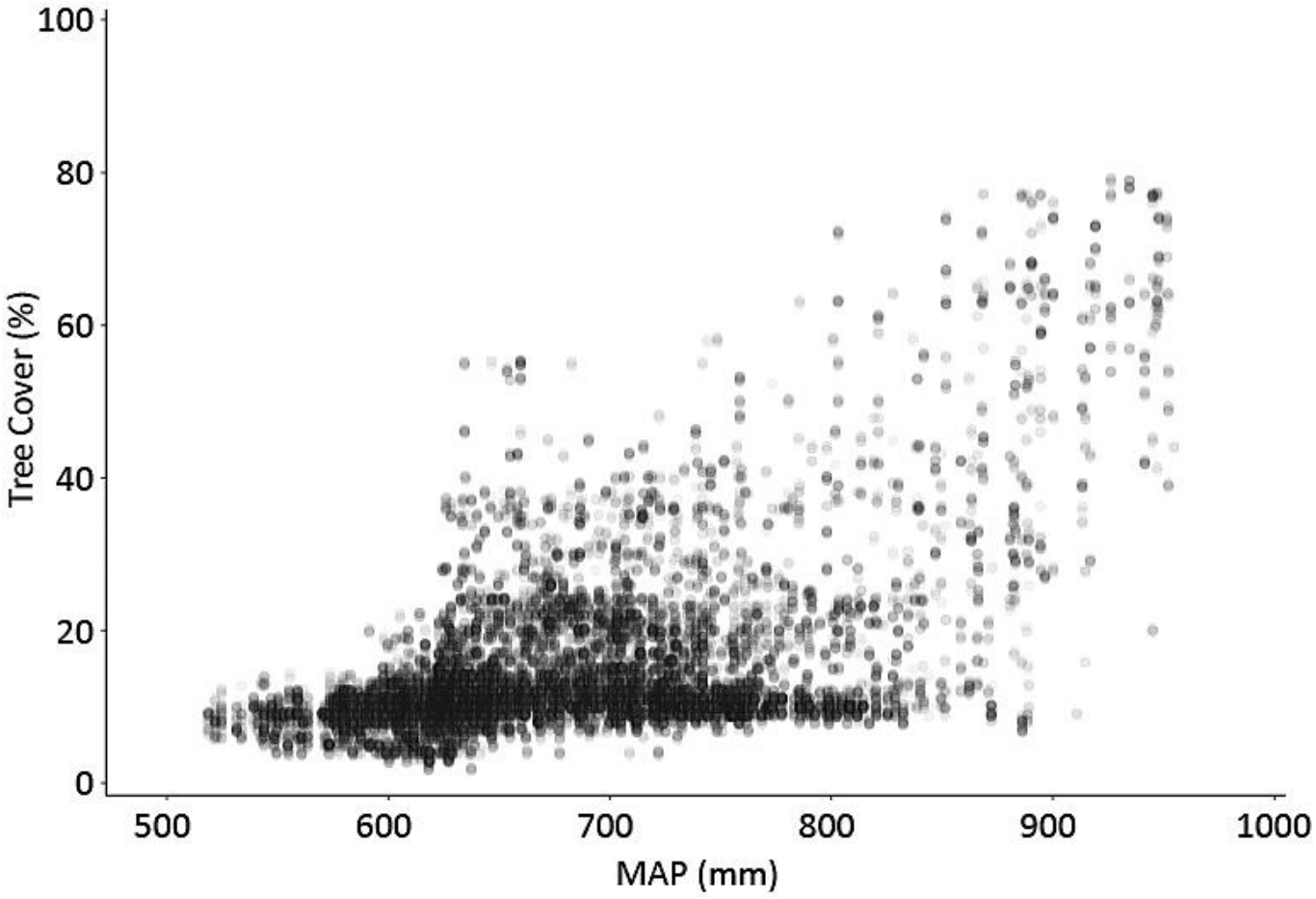
Conclusions

I tested the hypothesis that fire behaviour accounts for the historical distribution of forests. The predicted fire spread in the mesic landscapes of Hluhluwe were compared with forest distribution in 1937 when fires were least constrained by management. My approach was mechanistic rather than correlative in that the fire model was based on physical principles of fire spread. The results support fire being the major factor determining forest distribution at that time. Conceptually, I know of no similar studies that predict the distribution of vegetation based on mechanistic effects of topography and wind on fire behaviour. I believe this mechanistic approach is novel and offers a new method for testing the Alternative Stable States hypothesis where the states involve fire-promoting versus fire resisting vegetation states.

4.6. Appendix

Appendix Table S4.1. Model statistics for generalized linear models. The model components are wind direction (NORTH, SOUTH, EAST and WEST) and elevation (DEM). Model selection was based on the Akaike Information Criterion. The dependent variable for all models is the presence of closed canopy vegetation.

Model	dAIC	Df	Weight	Resid.dev
NORTH + DEM	0	3	1	94866.6
SOUTH + DEM	2218.1	3	<0.001	92722.1
NORTH	10558.8	2	<0.001	82161.3
EAST + DEM	12502.3	3	<0.001	104845.7
WEST + DEM	12534.3	3	<0.001	94663.6
DEM	12703.3	2	<0.001	94881.1
SOUTH	12717.8	2	<0.001	84379.4
EAST	22682.4	2	<0.001	104927.2
WEST	22763.9	2	<0.001	94695.6



Appendix Figure S4.1. Relationship between Tree Cover and Mean Annual Precipitation for the Hluhluwe section of Hluhluwe iMfolozi Park. Tree Cover data are derived from Hansen *et al* (2013).

Chapter 5

The aftermath of a firestorm

Recurrent fires are vital for biome switches in a mesic savanna-forest mosaic after a firestorm

5.1. Abstract

Forests and savannas in a savanna-forest mosaic are maintained by positive feedback loops with fires. Frequent fires in savannas create demographic recruitment and establishment bottlenecks preventing increases in tree cover and promoting flammable grass productivity. Forests, on the other hand, form dense canopies which shade out C4 grasses and create a humid microclimate, thereby reducing the available fuel load and suppressing fires. Occasional extreme fires do however burn into forest edges and cause extensive mortality. The response of forest and thicket vegetation to these extreme fires is poorly understood, limiting understanding of fire as a driver of biome-level change (rather that biome bistability). Are the changes in vegetation communities seen after extreme fires indicative of a switch between alternative stable states? Using an eleven year data set of repeat vegetation transects from both before and after extreme fires I investigate the stability of forest and thicket ecosystems after firestorms looking at tree and grass species composition, vegetation structure and changes in fire regimes. Forests recovered exclusively from pioneer species in the seed bank. Thickets recovered through basal resprouting, however no transects had a fire return interval long enough to allow for canopy closure. Extreme fires provide the opportunity for a biome switch from forest and thicket systems to savanna systems. However, the timing of subsequent fires is vital for the colonisation and establishment of flammable grass clades and a savanna fire regime.

Keywords: catastrophic regime shifts, Alternative Stable States, firestorms, forest, savanna, thicket

5.2. Introduction

Frequent savanna fires (several per decade) do not usually penetrate beyond intact forest margins. Thus it is not uncommon to find forest/savanna mosaics despite the potentially destructive impact of fire on forest trees. These mosaics are generally considered to be maintained by positive feedback loops with fires. While our understanding of these feedback loops offers insight into the existence of Alternative Stable States, there is a clear lack of research regarding the impact of extreme events on the spatiotemporal dynamics of these vegetation patches.

A leading hypothesis for the maintenance of alternative stable states in mesic savannas is that C4 grass fuelled fires are frequent enough to kill fire-sensitive saplings (forest saplings are particularly fire-sensitive). The conditions for stability are therefore: 1) fires are frequent enough to prevent forest recruitment into savannas, and 2) the fuels for fire are excluded in forest and thicket understorey conditions. We know that grass fuel is excluded in forests (Hoffmann et al, 2012a; Charles-Dominique et al, 2018), but then, why are forests not simply always expanding?

Savanna fires, characteristically, do not cross the boundary between biomes due to a sudden reduction in fuel, as shade intolerant C4 grasses disappear within meters of the boundary from savanna or grassland into thicket or forest (Hennenberg et al. 2006; Hoffmman et al. 2012; Charles-Dominique et al, 2018). The absence of grass fuels is usually sufficient to prevent a fire from burning into a thicket or forest. Forests and thickets have different microclimates to savannas with reduced wind speeds and increased fuel moisture (Biddulph and Kellman, 1998; Little et al, 2012, Hoffmann et al, 2012b) further reducing the likelihood of fire spread.

An important element to consider is the time-scale of stability: some boundaries seem stable over short to medium time-scales (ten to several hundred years) but have been proven to be unstable over longer time-scales, as inferred from isotopic evidence (West et al, 2001). Looking at extreme fire events - ‘firestorms’ - provides us with the opportunity to test Alternative Stable State concepts by investigating what happens in closed canopy systems that have been perturbed sufficiently to shift them out of their domain of attraction and into

another. Firestorms provide a destabilizing mechanism which could act as a driver of biome level change labelled a 'catastrophic regime shift' (Scheffer and Carpenter 2003).

A number of studies investigate biome shifts in systems where, due to fire suppression, savannas are converted into forests - through recruitment of fire-sensitive saplings (Bond and Parr, 2010) - however the inverse is rarely documented, or even observed. Unlike studies of burning in the logged forests of the neotropics, and the Amazon, the forests at HiP have natural boundaries with savannas and frequent savanna fires are the norm. 'Savannization' in the Amazon is typically studied in extensive patches of forest which have been logged, or where grasses have been planted by ranchers, so that the trees are likely to be completely 'naïve' to fire. In HiP forest patches naturally abut savannas, the system has its native herbivores, and human impacts are low. However, as is true for most of southern Africa, fires are usually lit by people pre-empting lightning fires which generally occur near the end of the dry season. Humans have been burning fires in the region for at least 150 ka with Iron Age farmers arriving in the area ~ 2 ka.

On the 14th and 15th September 2008 a firestorm occurred in the Hluhluwe section of the park and, unlike typical savanna fires, it tore through large tracts of thicket and forest. Events such as this are both rare and extreme which makes studying them, and the conditions necessary for their formation, difficult. Pioneering work, conducted in HiP, has helped to identify the conditions under which firestorms are thought to develop using the framework of Bradstock (2009), who identified a set of 'switches' that need to be 'flipped on' for a fire to occur. Using this approach, a set of switches was developed for firestorms at HiP (Browne and Bond, 2011). An analysis of the weather conditions preceding and during the 2008 fire conformed to a set of switches known as 30' 30' 30' conditions which allowed a surface fire to transition to an intense crown fire. Provided there is sufficient fuel that is adequately cured, and ignition occurs, a firestorm will develop if these three switches are 'flipped on'; the air temperature reaches above 30°C, the relative humidity falls below 30% and wind speeds averaging 25km/hr with gusts to 30km/h or more (Browne and Bond, 2011).

Three major firestorms have occurred in Hluhluwe iMfolozi Park since the beginning of this millennium. Prior to this there is scarce evidence of firestorms occurring, as demonstrated by the overwhelming bush encroachment in the park since the 1930s (Wigley et al, 2009). These

fires are unique in that, with relative ease, they crossed the boundary between biome types, consuming highly flammable grasses in savannas but switching to woody biomass and leaf litter fuels in forests and thickets. This effectively opened up the closed woody environment through the widespread mortality and topkill of adult trees (Browne and Bond, 2011).

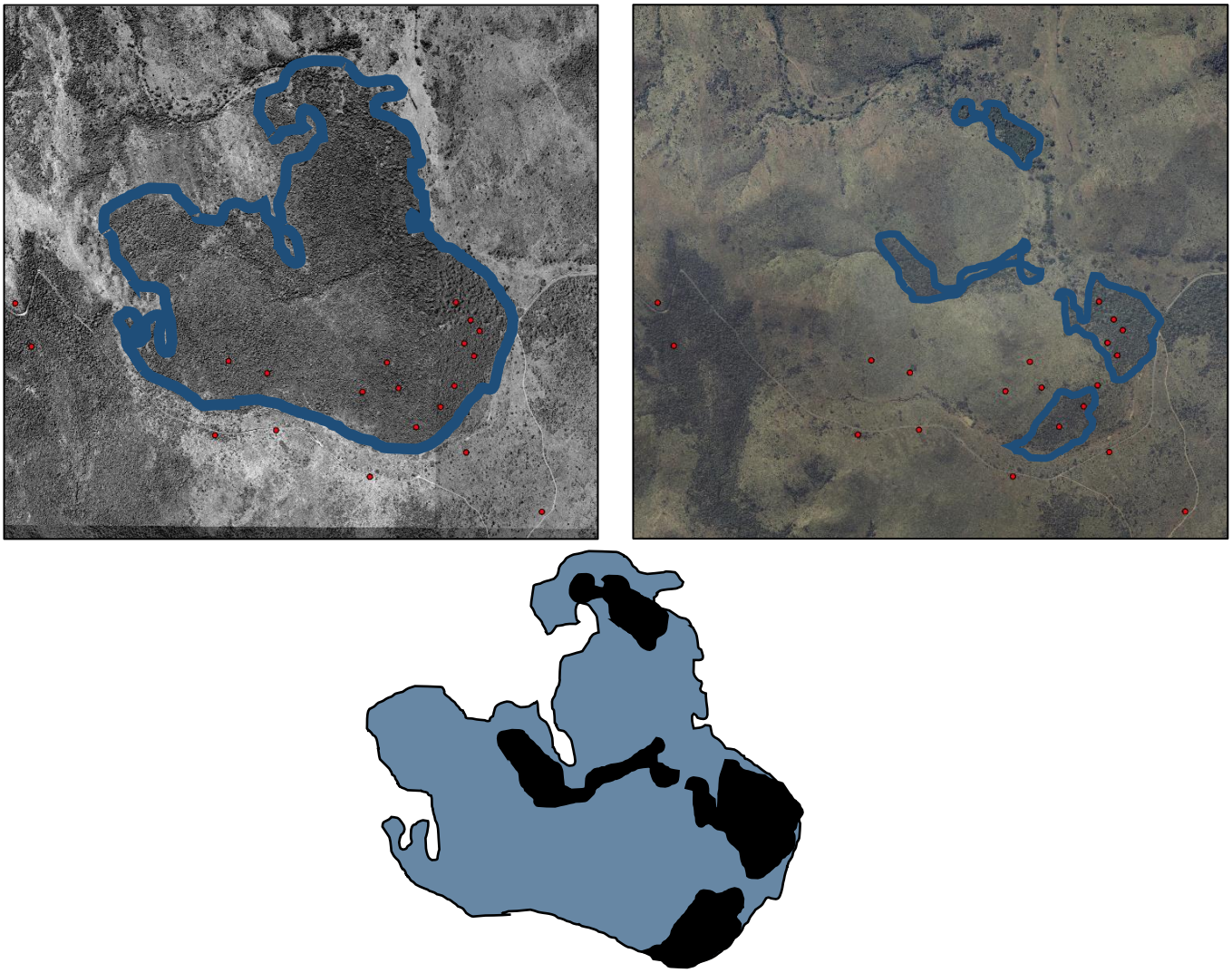


Figure 5.1. Aerial photographs (top) showing the extent of thicket vegetation in 2006, 2013 and the location of Zincakeni transects. The change in thicket patch extent (bottom) displays the magnitude of thicket loss (Blue = thicket in 2006, Black = thicket in 2013).

Catastrophic regime shifts occur in a range of systems: hypoxia/eutrophication of lakes, seagrass, peatland, mangrove, and kelp forest transitions, fishery collapse. What constitutes a biome shift in the context of a savanna-forest mosaic? In forests switching to savanna, we'd expect to see 1) a change in tree species composition (from shade-tolerant species that compete for light, to shade-intolerant species that occur in open environments and invest in protection from fire), 2) a reduction in tree cover and biomass, and 3) the establishment of a

regular fire regime (or the ability for a system to burn in the future i.e. sufficient grassy biomass). Since frequent fire is generally considered the key process maintaining savannas, colonisation of burnt forest by grasses producing sufficient fuel to carry a fire is an indicator that the threshold to a new stable state has occurred. If, however, trees recover and generate sufficient shade to exclude grasses and/or create a microclimate that inhibits fire spread, then the system has recovered from a major perturbation and will remain in a stable forest state.

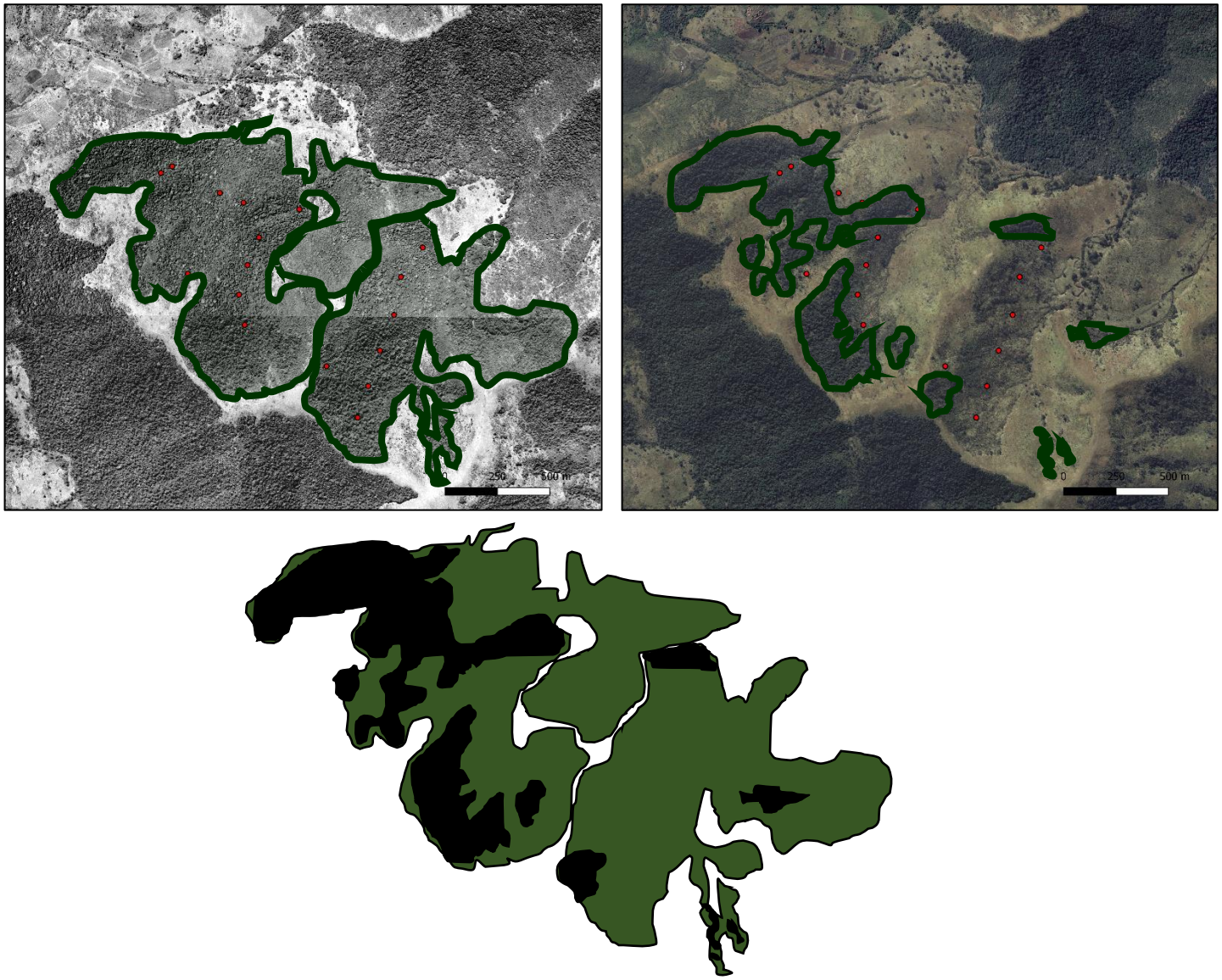


Figure 5.2. Aerial photographs (top) showing the extent of forest vegetation in 2006, 2013 and the location of Mpongo Forest transects. The change in forest patch extent (bottom) displays the magnitude of thicket loss (Green = forest in 2006, Black = forest in 2013).

As in most protected areas around the world, there are conflicting conservation and management objectives in HiP, such as combatting bush encroachment (through the use of

extreme fires) and the preservation of relictual forest patches (preventing savanna fires from crossing the boundary into forests). The response of forest and thicket vegetation to these extreme fires is poorly understood, limiting understanding of fire as a driver of biome-level change (rather that biome bistability). Extreme events, especially wildfires, are becoming more common globally due to greater variability in rainfall and increased temperatures (Jolly *et al*, 2015). Understanding the effects of these firestorms on vegetation dynamics is becoming increasingly relevant in the context of climatic change, particularly so in mosaics where landscape heterogeneity leads to a high diversity of specialized fauna and flora. In this study, I addressed the following questions: Are the changes in vegetation communities seen after these extreme fires indicative of a switch between alternative stable states? Do extreme fires have the potential to cause a catastrophic regime shift from one biome state to another? How resilient are non-naïve forest and thicket boundaries to fire?

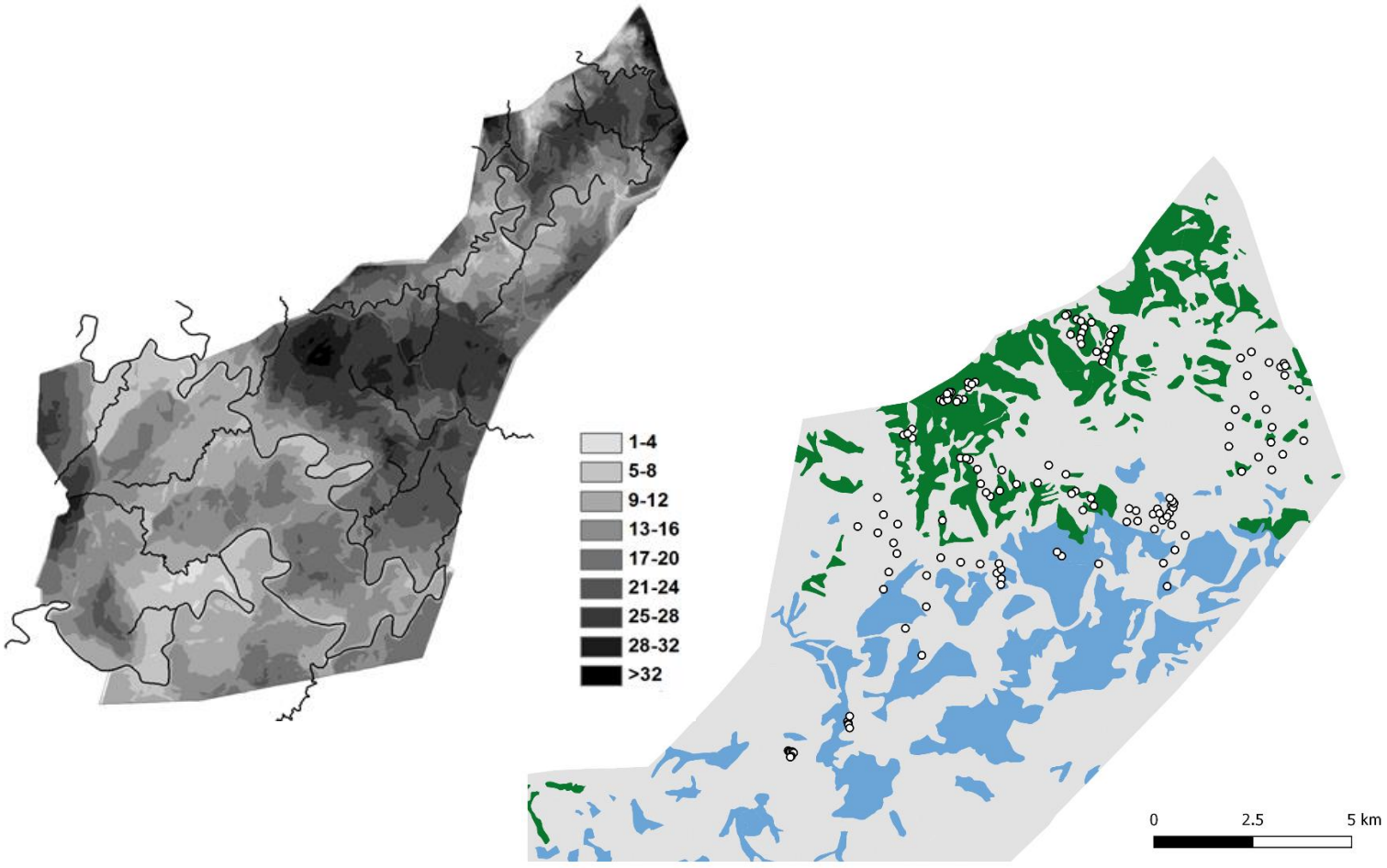


Figure 5.3. Fire Frequency map (left) of Hluhluwe iMfolozi Park from 1955 to 2013 based on Hluhluwe iMfolozi Park records and (right) the distribution of transects and biomes based on a reclassification of Whateley and Porter (1983). Reclassification based on Charles-Dominique *et al* (2015). Green = Forests, Blue = Thickets, Grey = Savanna and Grassland.

5.3. Materials and Methods

I restricted my investigation to a mesic system, the Northern section of HiP, an area that receives sufficient annual rainfall (Balfour and Howison, 2002) to support a closed canopy forest or thicket (Sankaran et al, 2005). The vegetation dynamics in this region are driven by fire, compared to the more arid, herbivore driven system in the iMfolozi section (Staver *et al*, 2009). Forest, thicket and savanna biome definitions (Box 1) are based on the classification scheme used in Charles-Dominique *et al* (2015), using vegetation structure and associated growth forms (Woodward et al, 2004; Ratnam et al, 2001).

Table 5.1. Summary of transect sites and sampling dates for tree species

Vegetation Type	n	Year Sampled	Resampled	n	Year Resampled
Savanna	51	2007	yes	44	2014
Intact Thicket	25	2014/2015	no	-	-
Frequently-burnt Thicket	12	2012	yes	12	2015
Forest	19	2014/2015	no	-	-
Frequently-burnt Forest	8	2012	yes	8	2015
	16	2014/2015	no	-	-
Recovering Forest	3	2012	yes	2	2015

Vegetation sampling

A total of 134 sites were sampled (Figure 5.3). 51 of which were first sampled by Staver *et al* (2007), and resampled by Case and Staver (2014) and 31 of which were sampled once each by Charles-Dominique et al (2015). I sampled the remaining 52 sites between 2012 and 2015. At each site a 40m by 10m transect was laid out. Within each transect, for every woody plant above 50cm in height, the species was identified, and height was recorded as one of four size classes (0.5-2m, 2-5m, 5-10m, and >10m). In 103 of the 134 sites, 20 disk pasture meter (DPM) readings, as well as the dominant grass species beneath the disk, were recorded at 2m intervals along two sub-transects in each half of the parent-transect. Transects were repeat sampled where possible. Transect sampling dates and repeat sample dates are summarized in Table 5.1 and Table 5.2. Transects were defined as intact, recovering, and frequently-burnt.

Intact forest and intact thicket transects were defined as forest and thicket patches that did not burn in the firestorms or any subsequent fires. Recovering forests burnt in one firestorm and have not burnt subsequently. Frequently-burnt forest and frequently-burnt thicket transects burnt in a firestorm and burnt repeatedly in the following years. Intact forest and thicket transects were laid out in mature vegetation patches, determined by comparisons with the vegetation map of Whateley and Porter (1983), and inspection of aerial photographs (Figures 5.1 & 5.2; *also see Chapter 3*).

Table 5.2. Summary of transect sites and sampling dates for grass species

Vegetation Type	n	Year Sampled	Resampled	n	Year Resampled
Savanna	51	2007	no	-	-
Intact Thicket	8	2009/2014	no	-	-
Frequently-burnt Thicket	12	2012	yes	12	2015
Forest	5	2014	no	-	-
Frequently-burnt Forest	8	2012	yes	8	2015
	16	2014/2015	no	-	-
Recovering Forest	3	2012	yes	2	2015

Fire frequency

The number of fires occurring in each transect from 2001 to 2016 was derived from a combination of the MODIS collection 6 MCD14DL active fire detections product and Ezemvelo KwaZulu Natal Wildlife (EKZNW, 2011) fire records for Hluhluwe iMfolozi Park. The MCD14DL product identifies thermal anomalies within 1km pixels using the MODIS MOD14/MYD14 Fire and Thermal Anomalies algorithm (Giglio, 2003). I used the MCD14DL product instead of the MOD45A1 burned area product to ensure fires in forests and thickets were detected, as burn scars following low severity fires can be obscured by a closed canopy. Active fire detections, combined with HiP fire maps, provided a measure of fire frequency in different vegetation types before and after firestorms.

Data analysis and statistics

Aerial photography and vegetation maps were analyzed using Quantum GIS 3.0.0 (Quantum GIS Development Team, 2018). Statistical analyses were performed in R (version 3.4.0, R. Core Team, 2017), using the packages *vegan* (Oksanen *et al*, 2013) and *tidyverse* (Wickham, 2017). Fire return intervals before and after firestorm events were compared using a Wilcoxon signed-rank test for non-parametric paired data. The biomass of dominant grass species was compared using the DPM calibration of Waldram *et al* (2008). I performed an NMDS Ordination on a Bray-Curtis species dissimilarity matrix of the cumulative length of tree species (Fei *et al*, 2005; Charles-Dominique *et al*, 2015). Cumulative length is a measure of the importance value of a species. Since length is related to stem diameter, cumulative length is a rough proxy for total basal area or biomass of a species in a sampling unit. Data were transformed using a Hellinger transformation to account for large abundances (Legrende and Legrende, 2012). Species were then assigned to a specific biome, based on their association with sites in the NMDS ordination, and used to identify compositional changes.

5.4. Results

Establishment of a savanna fire regime

Forests and thickets rarely burn with untransformed intact forest and thicket sites (sites not burnt in the firestorm) having no fires between 2000 and 2016 (Figure 5.4). Savanna sites had a significant increase in their fire frequency (FF) from approximately one fire every four years (FF = 0.24±0.11 before 2008 firestorm) to one fire every three years (FF = 0.36±0.13 after 2008 firestorm, N = 51, $p < 0.05$). Thicket patches that burnt in the 2008 firestorm quickly established a savanna fire regime with sites burning on average once every three years (FF = 0.34±0.07), compared to no fires from 2000 to 2007. Forest sites that burnt were split into two groups, those that burnt only once which I have called "Recovering Forests", and "Frequently-burnt Forests", those that burnt in a firestorm and have since burnt on average once every four years (FF = 0.26±0.04, Figure 5.4). These groupings are confirmed by changes in grass and tree species, biomass and structure.

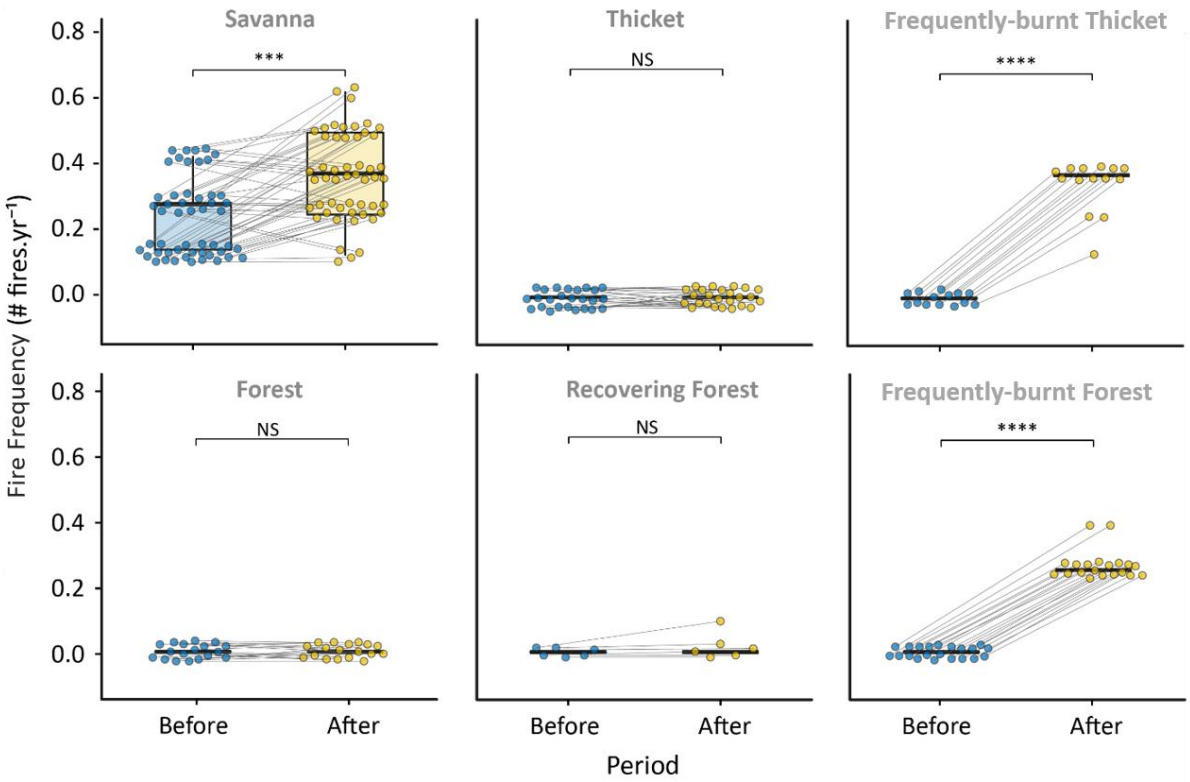


Figure 5.4. Fire Frequency for transects within each vegetation type (indicated by grey text) before and after firestorms (not including the firestorm), calculated using the MODIS Active Fires Product. Grey lines link transect points before and after firestorms. Asterisks indicate significance level (*** <0.05, **** < 0.001, NS = no significant difference).

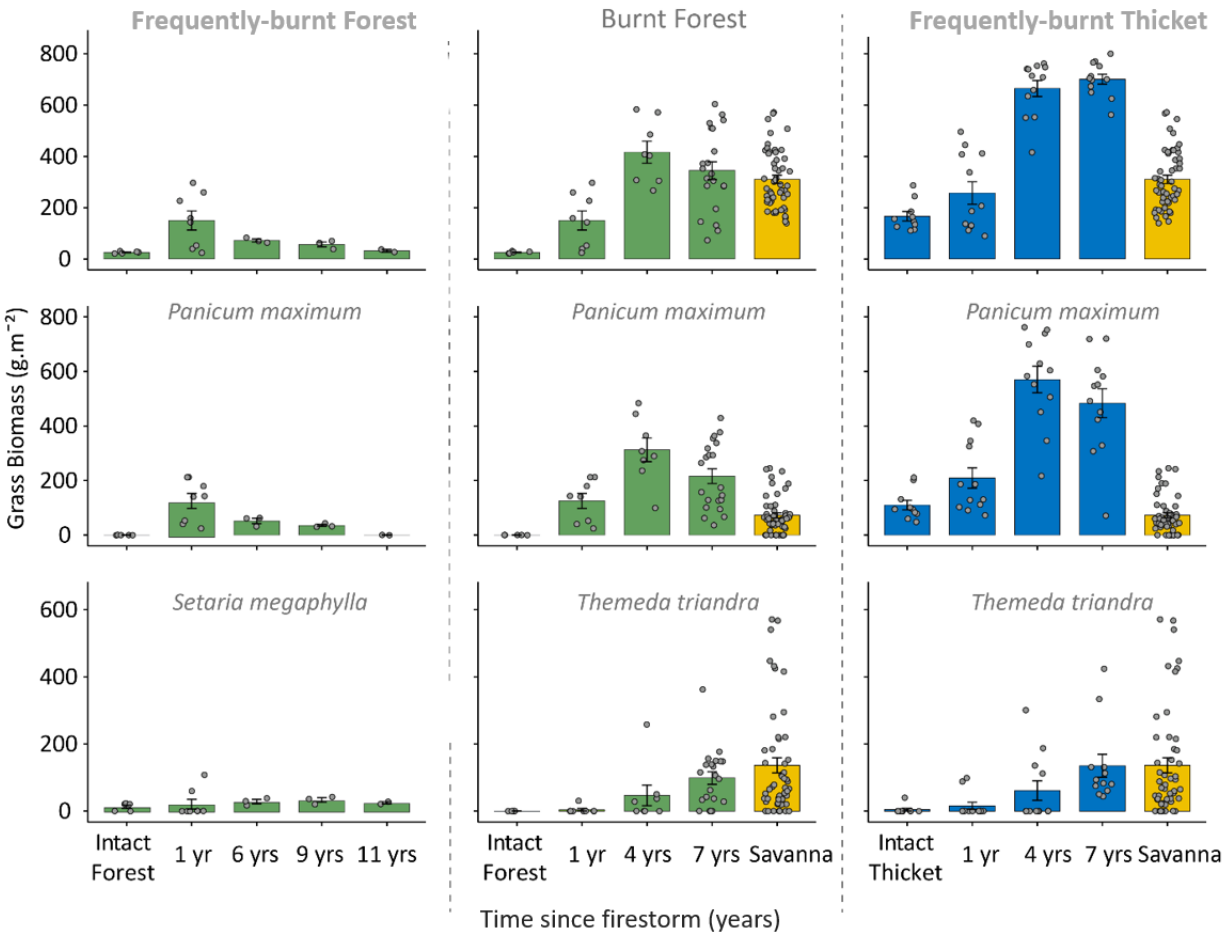


Figure 5.5. (Top row) Changes in biomass of the grass species found in all transects for forests that burnt once (recovering forest), forests that burnt multiple times (frequently-burnt forest) and thickets that burnt multiple times (frequently-burnt thicket). (Middle and bottom row) Grass biomass of the two dominant species in each vegetation type. Green bars represent forest transects, blue represents thicket, and yellow represents savanna. Savanna grass biomass (yellow bars) is included for comparative purposes only. Error bars indicate standard error. Points (individual transect grass biomass) are included to display variation.

Colonisation by savanna grasses

Intact thicket and forest transects were distinct from savanna transects in that they have closed canopies and little or no grass in the understory. Savanna transects had on average 470 $g.m^{-2}$ of grass biomass whereas thicket and forest patches had 212 $g.m^{-2}$ and 34 $g.m^{-2}$ respectively (Figure 5.5). Both frequently-burnt thicket and frequently-burnt forest transects showed an increase in grass biomass following successive fires, with grass biomass five and fifteen times higher than that found in intact thicket and forest transects respectively (Figure

5.5). Recovering forest transects had high grass biomass (300 g.m^{-2}) in the first year after the firestorm, however this decreased over time, with grass biomass and composition dropping to 38 g.m$^{-2,}$ similar to intact forests by the end of the study, 11 years later. Increasing grass biomass was associated with an increase in, initially, *Panicum maximum*, followed by *Themeda triandra*, with increased burning (Figure 5.5).

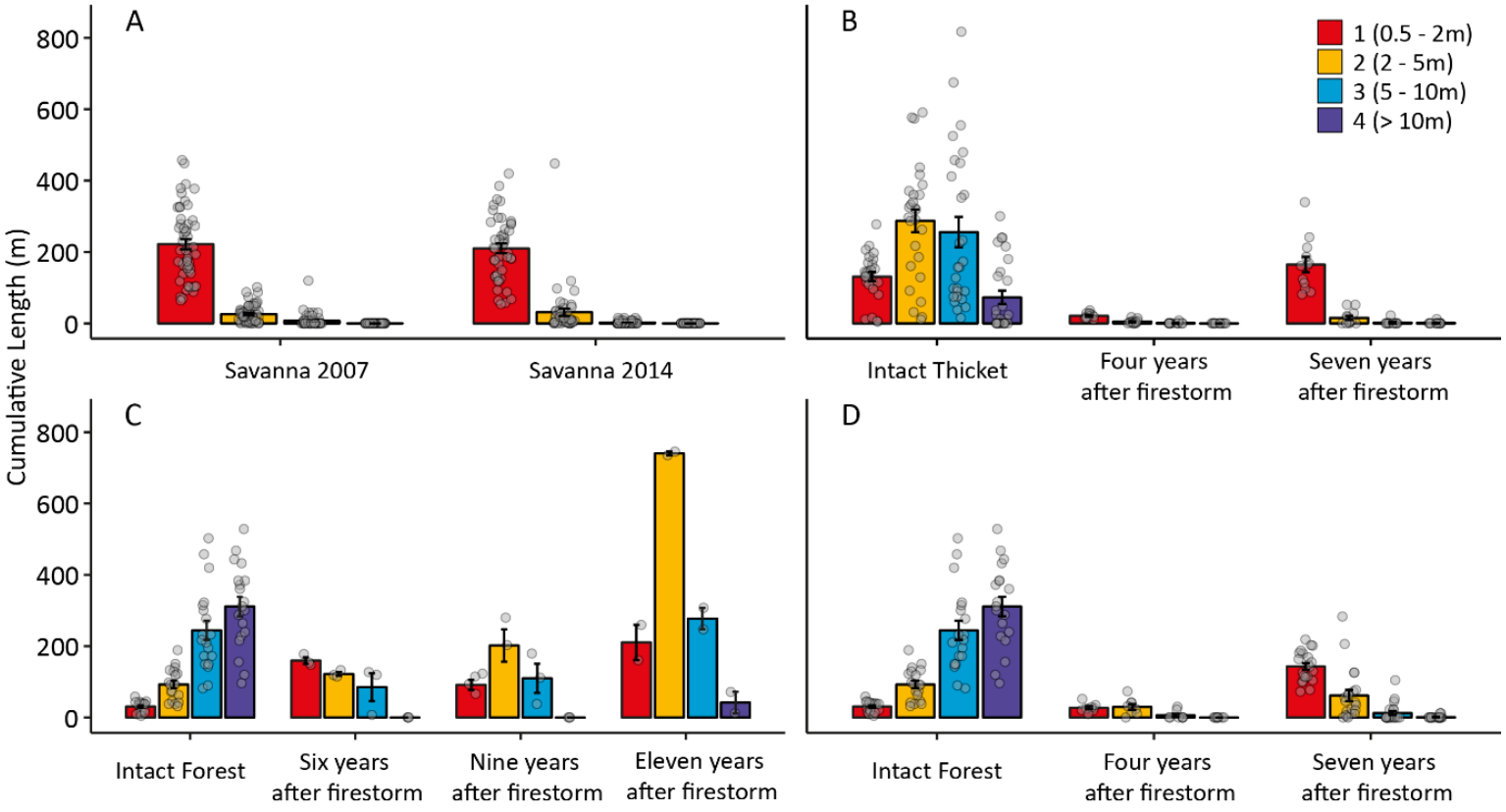


Figure 5.6. Mean cumulative length of all tree species within the four size classes in A) Savanna, B) Frequently-burnt Thicket, C) Recovering Forest, and D) Frequently-burnt Forest. Error bars indicate standard error. Points represent individual transects. All transects are 400m^2.

Woody structural changes

Forest, thicket and savanna transects displayed distinct structural profiles, with the majority of savanna biomass (represented by cumulative length of tree species) in the smallest size class, most forest biomass in the largest size class, and an even spread between the two intermediate size classes in thicket (Figure 5.6). Savanna transects showed little change in structure between the two time periods despite an increase in fire frequency. Thicket

transects that burnt were almost unrecognizable four years after the firestorm, with most biomass in the first size class, and a similar structure to savanna transects seven years later. The same is true for forest transects that burnt multiple times, which resembled savannas structurally, with most biomass in the first size classes.

Woody compositional changes

Forest, thicket and savanna transects had distinct species assemblages (Figure 5.7). This was evident when using the total cumulative length of each species as a measure of abundance, and the individual size class cumulative lengths (i.e. thicket transects do not show evidence of succession towards forest). Frequently-burnt thicket transects did not have a unique species assemblage, generally being a mix of basally resprouting thicket species - such as *Euclea racemosa, Euclea divinorum* and *Berchemia zeyheri* – and an increasing proportion of savanna species, e.g. *Acacia karroo, Acacia nilotica, Dichrostachys cinerea, Cordia caffra, Combretum molle* and *Rhus pentheri*, with successive fires (Figure 5.8).

Frequently-burnt forest transects were dominated by pioneer forest species seldom found in the climax/intact forests (i.e. *Trema orientalis, Croton sylvaticus, Dombeya burgessiae*). These trees grew from seed banks, as opposed to the basally resprouting dominants in frequently-burnt thicket transects. Four years after the firestorm frequently-burnt forest transects were dominated by a number of thicket species such as *Euclea natalensis* and *Euclea racemose* and had low biomass in all size classes. Recovering forest transects had a number of climax forest species after 11 years such as *Englerophytum natalense* and *Chaetachme aristata* in the smaller size classes, although the larger size classes were still dominated by a unique pioneer forest assemblage.

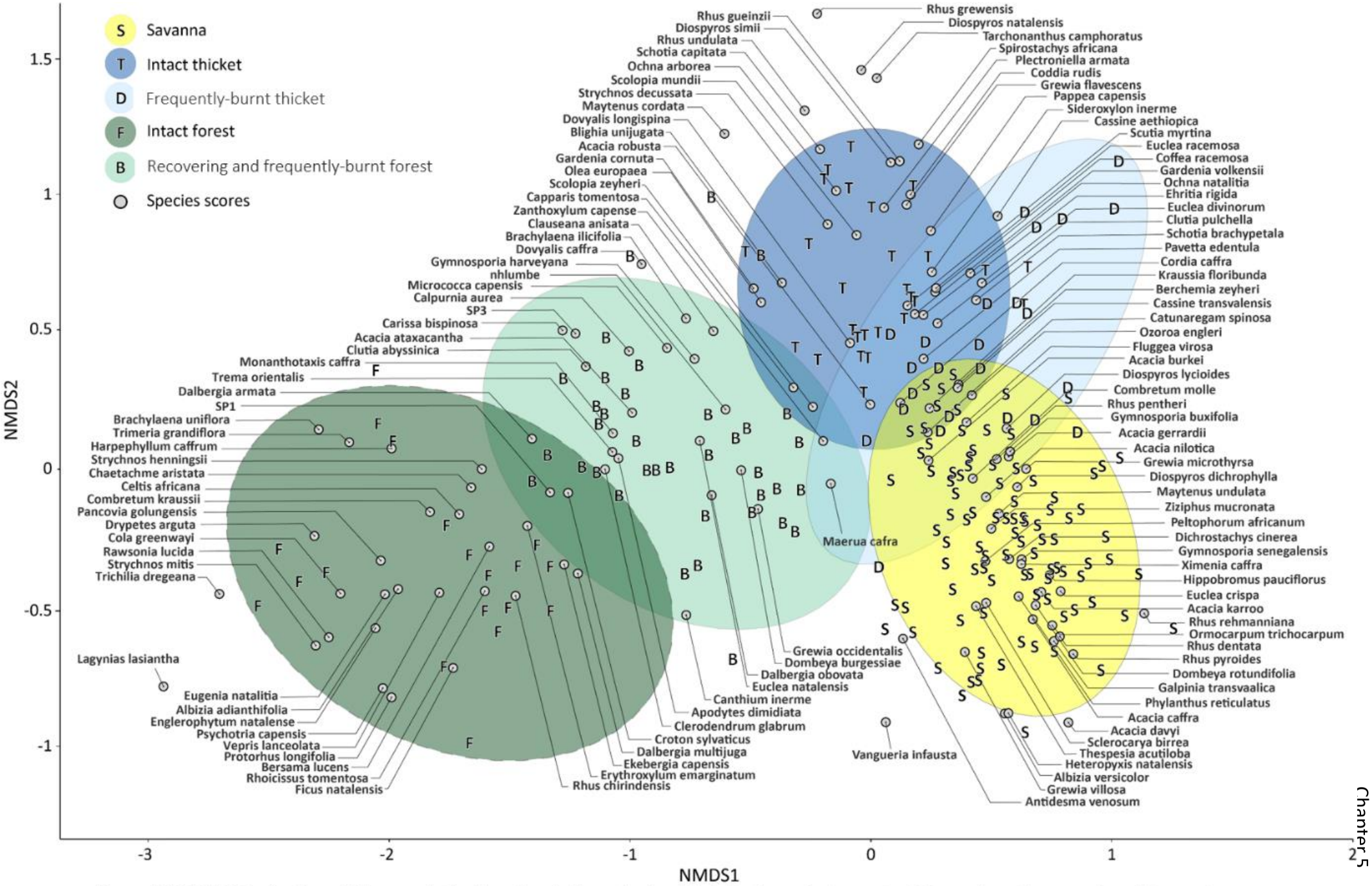


Figure 5.7. NMDS Ordination of the cumulative lengths of all species in all height classes in transects. Ellipses show the grouping of transects. Species associations used in Figure 8 are based on species found in transects before firestorms only. Letters indicate the position of transects, grey dots indicate the species scores.

5.5. Discussion

Extreme fires, as observed in HiP, provide an opportunity for a biome switch from closed, fire intolerant forest and thicket systems to open fire dependent savanna systems. However, the timing of subsequent fires is vital for the colonisation and establishment of flammable grass clades and a savanna fire regime. A fire free interval allowing for the recovery of a canopy, which in turn shades out these fuels, will allow a system to return to its previous state.

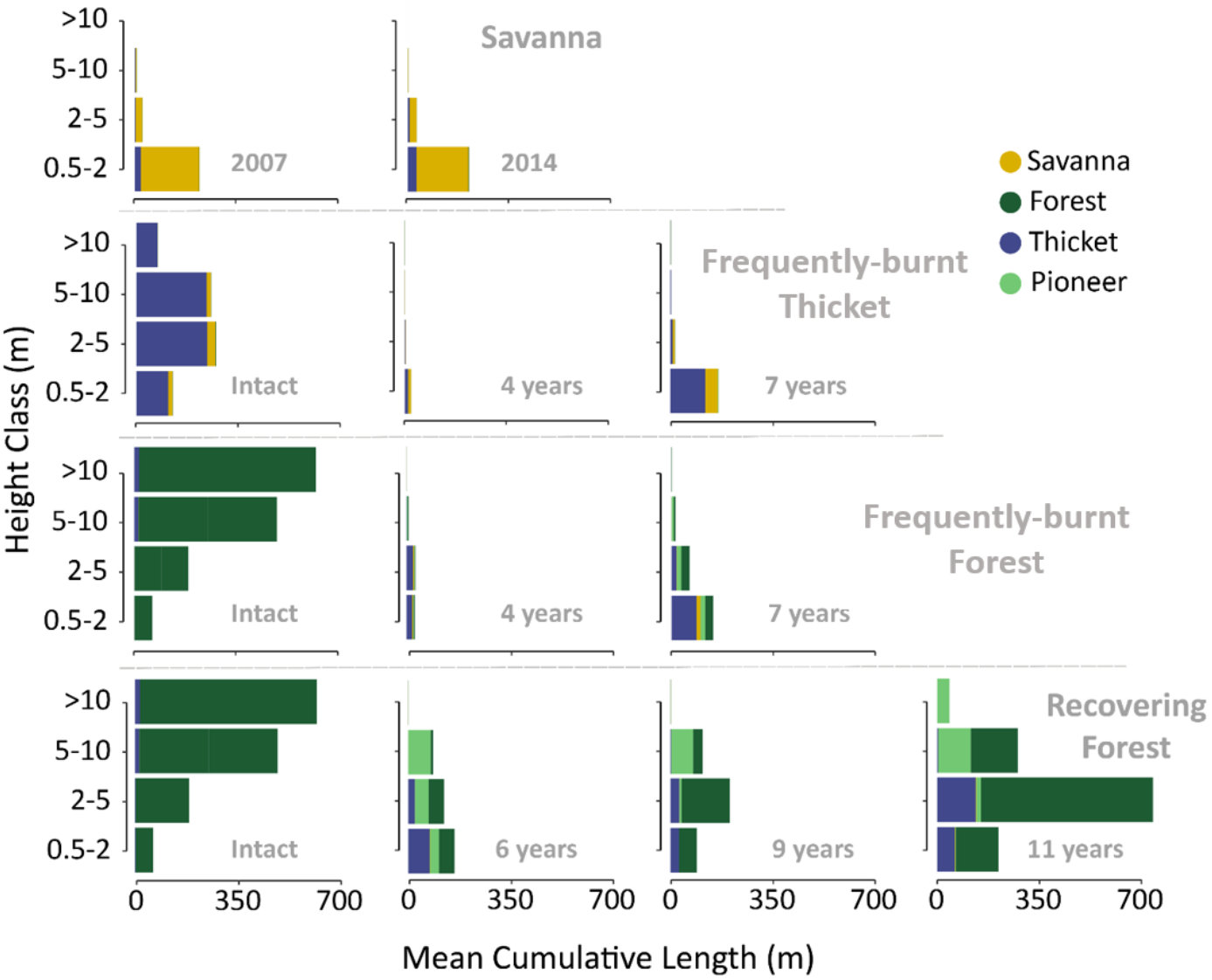


Figure 5.8. Initial and final composition and structure of savanna, frequently-burnt thicket, frequently-burnt forest and recovering forest. Panels display the average cumulative length of tree species within each size class for the different time periods after firestorms, denoted by grey text. Colours indicate the biome in which these species are predominantly found. Pioneer species are those which were not found in transects sampled before the firestorm.

The firestorms in Hluhluwe burnt into both thicket and forest patches. While in the thickets we have observed the recovery of trees through basal resprouting, in the frequently-burnt forests we have seen a complete species turnover. Tree mortality following fires is much greater in forests than in savannas and thickets, despite similarities in the bark thickness of tree trunks. Forest trees do not seem to reach the 'fire-resistance threshold' proposed by Hoffmann et al (2012); instead the emphasis is placed on reaching the 'fire-suppression threshold' where canopy shading excludes flammable grasses.

Following a firestorm, forests recover from a seed bank after which there is a successional pathway, distinct from the pathway in a tree fall gap. Tree species establishing from a seedbank after the forest fire were rapid-growing pioneer forest species (i.e. *Trema orientalis, Croton sylvaticus, Celtis africana*) and the clonally spreading liana, *Dalbergia armata*. These species established a microclimate/environment suitable for climax forest species to establish and cast sufficient shade to exclude light-demanding grasses.

Grass clades differ in productivity, as well as moisture retention throughout the dry season. *Panicum maximum* (Paniceae) is often observed in shaded environments, and is known to retain moisture longer into the dry season, whereas *Themeda triandra* (Andropogoneae) prefers open, full sun environments (Downing and Marshall, 1980; Kinyamario et al, 1995). *Themeda triandra* is a highly flammable savanna grass and, although it is slow to colonise new environments, within seven years it was frequently seen in the burnt thicket and burnt forest transects. The appearance of a 'savanna grass' within these transects (Charles-Dominique et al, 2018), with similar biomass to that in savanna transects, along with the establishment of a regular fire regime, is evidence of a shift from a closed system to what is functionally and structurally an open system.

Whether or not these systems have switched to a savanna compositionally is more complex. Savanna transects that burnt in the 2008 firestorm showed very little compositional shift (Figure 5.8). Case and Staver (2017) show this is the case for savannas across HiP with very little compositional change, only a reduction in larger savanna trees in areas with higher than historical fire frequencies. Parr *et al* (2012) showed certain areas had transitioned from open savannas to closed thickets, which led to a change in the dominant ant species. I show here how these thicket systems reverted to open systems (Figure 5.9a), structurally resembling a

savanna, although compositionally still dominated by thicket species that were able to basally resprout (see Figure 5.9b). A regular savanna fire regime will presumably deplete these species, by reducing their ability to resprout, and eventually replace thicket species with savanna species better suited to this environment (Charles-Dominique *et al*, 2015).

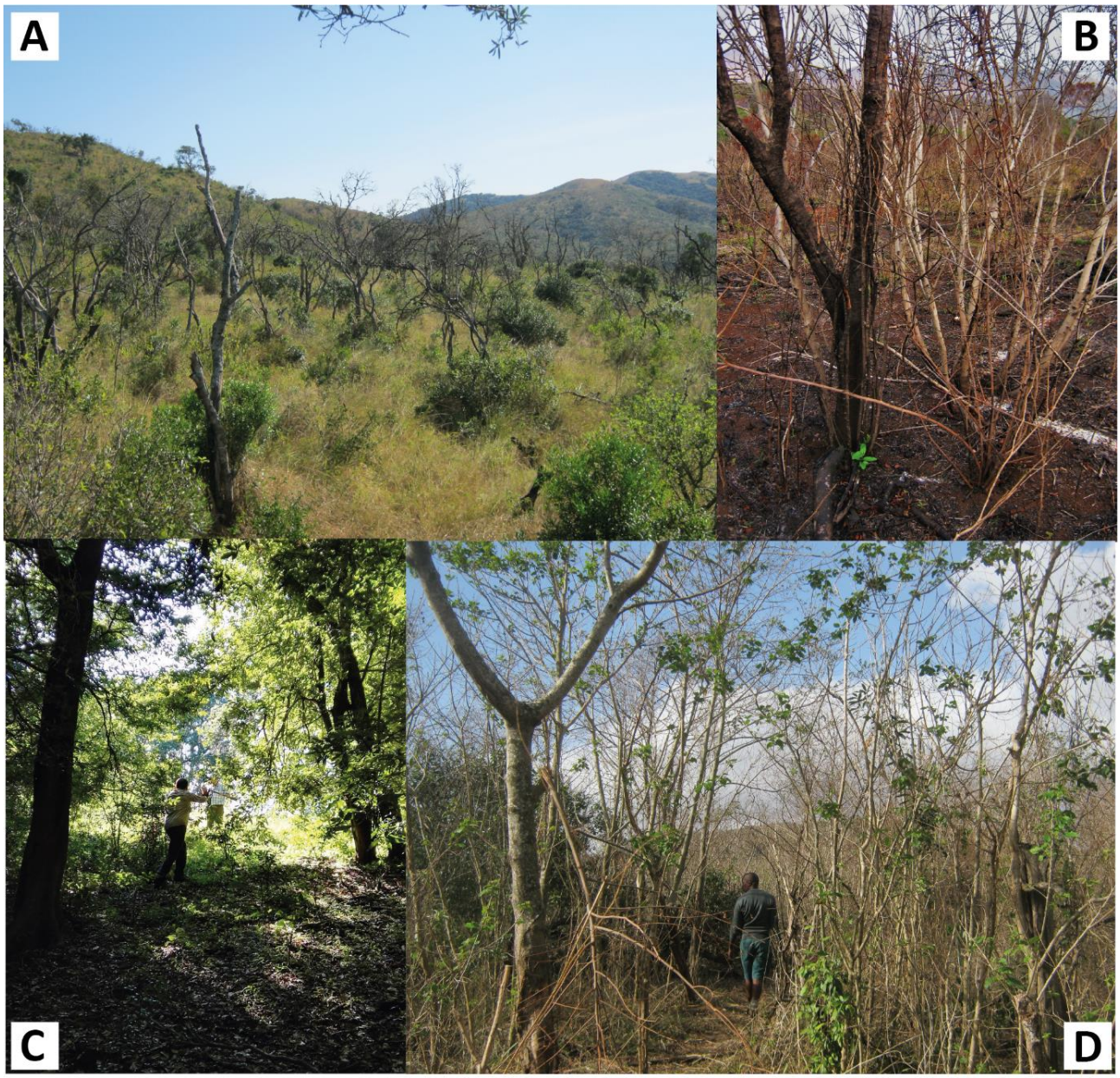


Figure 5.9. Photographs showing A) Frequently-burnt thicket patches with high grass biomass, and small basally resprouting trees. B) Thicket tree species basally resprouting after a third fire, *Berchemia zeyheri* on the left, *Euclea racemosa* on the right. C) An intact forest-savanna boundary (held in place by Yadvinder Malhi and William Bond). D) A nearby recovering forest patch burnt 9 years before, showing deciduous pioneer species forming the canopy and evergreen climax species establishing in the understory where grasses have been suppressed.

Despite the benefits they offer in combatting bush encroachment, the difficulty in applying firestorms as a management tool lies in the nature of firestorms; they are extreme events. An attempt in Kruger National Park to create a firestorm in 2010 (Smit et al, 2016) was successful to the point that it burnt out of control, killing one rhino and causing a public outcry. Herein lies the issue, once the 'switches are flipped on', it is very difficult to turn a firestorm off. The uncertainty of the future of firestorms and how this will affect forests is an important area of research. The conditions necessary for a firestorm to develop, air temperatures above 30°C, relative humidity below 30% and wind speeds of approximately 30km/h, are exceedingly rare. Over the period of 2001 to 2008, less than three days of 30' 30' 30' conditions occurred, with the longest consecutive record of 11 hours occurring on the day of the firestorm in 2008, the 15th September (Browne, unpublished thesis). The required amalgamation of these 30' 30' 30' conditions with sufficient fuel and an ignition event make firestorms difficult to predict and even harder to forecast into the future.

Concerns over the use of firestorms in HiP surround the potential for these fires to wreak havoc in fire-sensitive indigenous forests. A meagre 0.1% of South Africa, of a potential 7%, is covered by indigenous forest (Mucina and Rutherford, 2009) and the high levels of biodiversity of Scarp Forest (six endemic genera and one endemic family of trees), found in HiP, is reason enough for this concern. In Chapter 3 I showed how forest vegetation is restricted to areas of lower fire danger, the importance of neighbourhoods and patch size dynamics, and how expansion and contraction occurs along this gradient. In Chapter 4 I showed how these fire refugia shrink when fires are burned under extreme conditions. It is clear from this study that firestorms have the ability to precipitate a biome switch. However, regular fires following the firestorm are needed to ensure the switch from a thicket or forest system to a savanna or grassland system. The probability of these subsequent fires burning into fire refugia are low, provided burning takes place in the 'correct' season under low intensity conditions.

Preface: Chapter 6

This chapter is structured differently from the preceding chapters as it has been written up in short format and is to be submitted for publication in *Ecology Letters*, *Science* or *Nature*. The analysis was initially focused on differences in functional traits between forest interior, forest edge, forest pioneer, and savanna tree species. The idea was conceived by Heath Beckett and Carla Staver who also collected the data Hluhluwe iMfolozi Park. The manuscript was rejected by reviewers due to a lack of sufficient data to substantiate the claims. In light of this critique we collected published data from the literature and contacted the data contributors (See Extended Data Table S6.1), which I assembled into a database of 934 species. Although this remedied our data problem, I was no longer able to investigate the differences between forest interior vs forest edge/pioneer species, and had to relax the categories to biome level differences. I was also no longer able to use the data I collected on post fire resprouting ability in Hluhluwe iMfolozi Park. Instead those data were published separately (Charles-Dominique *et al*, 2015; *citation below*), and the topic of this chapter shifted focus to a more global issue.

CHARLES-DOMINIQUE, T., BECKETT, H., MIDGLEY, G. F. and BOND, W. J. 2015. Bud protection: a key trait for species sorting in a forest-savanna mosaic. *New Phytologist*, 207(4), 1052-1060.

BECKETT, H., WRAGG, P., CHARLES-DOMINIQUE, T., [data contributors…], and STAVER, A. C. (In prep). Among plant functional traits, bark and height primarily differentiate tropical trees.

Data contributors:

J. Barlow, I. Oliveras, B. Wigley, T. Ibanez, S. Fauset, E. Gray, S. Bowers, C. Geldenhuys, B. Wolfe, A. Cardoso, W.J. Bond, S. Syampungani, V. Williams, Y. Malhi, A. Murakami, C. Ryan*

*At the time of thesis submission, data ownership and authorship has not been decided upon, hence the lack of some publication details in Table S6.1

Chapter 6

Among plant functional traits, bark and height primarily differentiate tropical trees

6.1. Introduction

Plant functional traits have been used effectively as simple proxies for ecological plant characteristics that are more challenging to measure (Diaz et al. 2004; Reich 2014). Traits may be constrained, both by developmental trade-offs (e.g. plants can only grow either quickly or slowly, with concomitant effects on longevity (Wright et al, 2004; Chave et al, 2009)) and by ecological trade-offs (e.g. savannas experience either intensive herbivory or frequent fires, seldom both (Staver et al. 2012)). Extensive synthesis has shown that plants are universally constrained by allocation trade-offs: leaves that have high rates of photosynthesis are short-lived and vice-versa (Reich et al, 1992; Wright et al, 2004), wood can either accumulate quickly and be short-lived or accumulate slowly and live long (Chave et al, 2009), and plants must strategically allocate limited carbon to leaves, shoots, roots. (Enquist and Niklas, 2002). However, the ecological trade-offs among plant functional traits are much less well understood.

This limited perspective on functional traits has real implications for our understanding and predictions about ecosystem functioning and species distributions. Dynamic Global Vegetation Models (DGVMs) are useful tools for predicting future vegetation distributions and the potential carbon storage and sequestration these changes might bring. By reducing the complexity of species composition in biomes to a set of plant functional types (PFTs) - which, theoretically, respond in a predictable manner to biotic/abiotic factors – DGVMs are able to predict the distribution of biomes across the globe. They are, however, notoriously bad at predicting the distribution of chronically disturbed systems, such as mesic savannas and grasslands, when disturbance is not accounted for (Bond, 2005). To address this problem we need to ask which traits are best suited to understand species sorting and vegetation structure where consumers (‘disturbance’) prevent a system from reaching its climate potential (Bond, 2005).

Existing global PFT syntheses have tended to examine plant functional strategies through the lens of competition (Diaz et al, 2016). In order to fully understand the ecological trade-offs in allocation it is necessary that we understand what happens in systems where succession and competition (for light) are not the dominant ecological processes (e.g. savannas) and identify traits that differentiate these systems. The plant economics spectrum (Wright *et al*, 2004;

Reich, 2014), capturing the co-ordination of multiple traits associated with rates of resource capture and retention, is widely used in understanding variation in vegetation responses to availability of nutrients and climate. Previous work has shown how the plant economics perspective is expressed as different life histories within forests (Westoby and Wright, 2006; Wright et al, 2004; Reich 2014).

High specific leaf area (SLA) and low wood density are readily-measured traits that indicate plants on the "fast" end of this spectrum, and predict high rates of photosynthesis, growth, and decomposition. Conversely, low SLA and high wood density, plants at the “slow” end of the spectrum, are indicative of low growth rates and usually interpreted as conferring leaf and stem longevity (Wright et al, 2004; Diaz et al, 2004; Chave et al, 2009). Specific leaf area and wood density do not covary, in that species do not occupy the full range of strategy space, and are constrained to a handful of successful plant functional types, as synthesized above (Diaz et al, 2016; Westoby and Wright, 2006). However, this focus on competition overlooks traits that are of critical importance in some widespread systems, where tolerance or avoidance of disturbances structures plant strategies and ecosystem function.

Within temperate and tropical forest biomes, traits are a useful way of quantifying species differences, including those related to successional stage such as plants growing in high light environments versus those in deep shade. Falster and Westoby (2003), along with others, assumed that the tree growth form evolved where plants competed for light so that, essentially, trees would not exist unless there was a risk of being shaded out by a neighbour. Thus, naturally, trait research centred on how plants compete for light and how they cope with shade. Vast areas of open non-forested habitats exist where trees do not necessarily have neighbours – including savannas, grasslands and shrublands. The question arises why, if selection for the growth form is about growing tall enough to compete with your neighbour (Falster and Westoby, 2003), be a tree in open habitats? And, how do trees diverge in traits in forests where light is the main axis of natural selection versus consumer-controlled non-forest systems where fire and/or herbivory are common determinants of tree densities and size structure (Bond, 2005)?

Some have argued that, between disturbances, chronically disturbed ecosystems are characterized by succession towards a climatically defined equilibrium (Archer et al. 1988; Sankaran et al. 2005). Others have argued that chronically disturbed ecosystems experience

disturbances so often that succession is not a dominant ecological process (Bond, 2008; Staver et al, 2011a). Extensive studies from the Brazilian cerrado have shown that savanna and forest are functionally distinct (Hoffmann, Orthen & Do Nascimento 2003; Hoffmann & Franco 2003; Rossatto, Hoffmann & Franco 2009) and these distinctions do not align with the fast-slow, leaf economics spectrum, early-late distinctions discussed above (Rosell et al, 2014).

The transition zones between savanna and forest are often abrupt despite similarity in climate (Staver et al, 2011a). They are ideal systems to consider the ecological trade-offs of plant functional traits, and identify differences between plant functional types associated with disturbance (herbivory, fire, drought) versus competition (light, resources). Savanna trees live in a flammable grassy matrix and are burnt at intervals of 1 – 3 years in mesic and humid regions (Hoffmann et al, 2009). Savanna trees are adapted to environments where light is reliably abundant (Archibald and Bond, 2003); instead, frequent fires filter out those species which do not invest in structures which resist fire damage (Higgins et al, 2012; Pausas, 2015; Charles-Dominique et al, 2015). Fires in forests, on the other hand, typically lead to much higher tree mortality than in savannas (Cochrane, 2003), although forests seldom burn due to a lack of grasses and a humid understory. An investment in fire resistance is known to be a trade-off against increase in plant size (Jackson et al, 1999; Hoffmann et al, 2003; Archibald and Bond, 2003). The ability to outcompete neighbouring plants for light is a vital trait for forest species (Jackson et al, 1999) so compromising on the rate of growth for increased defence against fires is an unnecessary precaution for plants that seldom burn (Jackson et al, 1999, Archibald and Bond, 2003).

Thick bark confers resistance to low-intensity fires (Uhl and Kauffman, 1990) and bark thickness is increasingly recognized as a key functional trait determining species' responses to fire regime (Hopkins, 1962; Pausas, 2015; Charles-Dominique et al, 2015), and may also be associated with other functions such as structural support and defence against consumers (Paine et al. 2010). However, it is not known how variation in bark thickness relates to widely recognized axes of variation such as the plant economics spectrum (Reich, 2014) and plant height (Westoby, 1998; Rosell, 2016). This is problematic as approximately 40% of the tropics is covered in savannas and we know investment in bark to be important for woody plant persistence in savannas.

Here, we compare functional traits across savanna and forests systems (see Figure 6.1a) in the summer-rainfall tropics and sub-tropics using a compiled database of over 25 000 individual trees, covering 934 species (see Figure 6.1b). We wished to determine whether traits associated with resource use were correlated with bark thickness, a trait related to fire resistance. Among resource use traits, we measured specific leaf area (known to vary among biomes and, within forest trees, to correlate with differences in photosynthetic rates (Sterck et al. 2006)), wood density (which again varies among biomes and predicts stem longevity among forest trees and correlates with growth rates (Chave et al. 2009)), and height (another size-varying trait, predictive of competitiveness for light (Purves & Pacala, 2008)). Bark thickness is unrelated to resource use but is a size-varying trait predictive of fire resistance (Hoffmann et al. 2003; Dantas & Pausas 2013, Lawes et al, 2013).

We were interested in determining how these traits vary across forest-savanna boundaries sharing similar physical site conditions (climate, soils) but varying greatly in vegetation structure and disturbance regimes. We expect these four traits to capture substantial, meaningful ecological variation among mesic savanna, dry forest and wet forest ecosystems. Moreover, we wished to explore the association, if any, between bark thickness and other traits in order to understand trait evolution in response to fire regime and other selective pressures such as herbivory and drought.

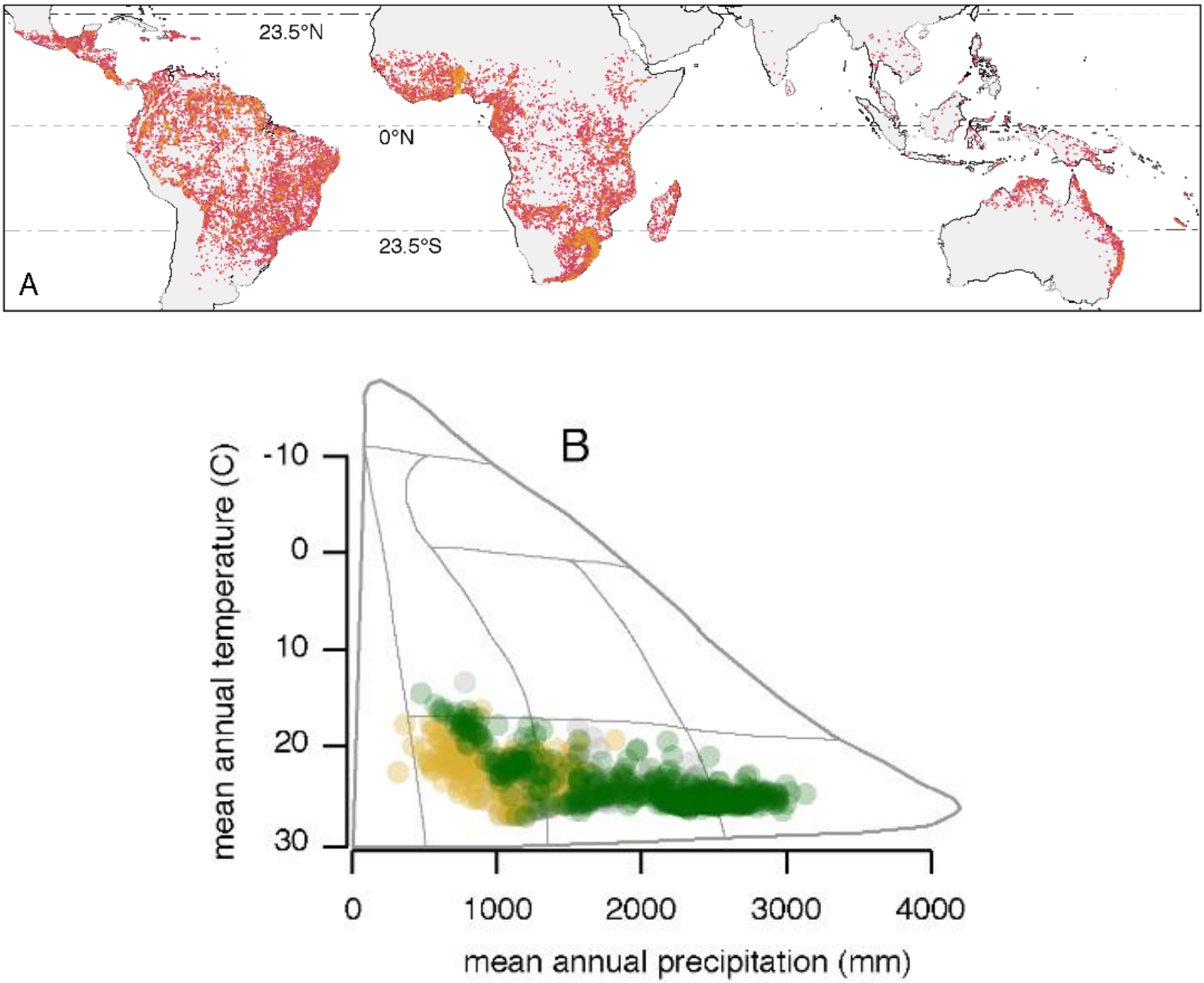


Figure 6.1. Heat map of global distribution of study species (a), occurrence according to GBIF (http://www.gbif.org), and (b) species level means for Mean Annual Precipitation and Mean Annual Temperature, overlaid upon Whittaker (1975) biome classification. Yellow – Savanna, Green – Forest, Grey – Unclassified

6.2. Materials and Methods

Database Assembly

We assembled a database of bark thickness and associated tree diameter measurements from authors, the literature and trait databases. Measurements of bark thickness were for total bark thickness, i.e., all material outside the wood (Pérez-Harguindeguy et al. 2013, Pausas 2014), between 30 cm and 130 cm above ground. Depending on the study, bark samples were extracted for measurement or bark probes were used to measure bark thickness in situ. Widely used standardized traits handbooks (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2013) have promoted consistency of methods, for this and the other traits. Because bark thickness scales with tree diameter, we compared species using their bark thickness allometric coefficient fitted to the raw data (where available).

For as many species with bark thickness data as possible, we obtained the following traits; plant height, specific leaf area and wood density. Plant height was measured to the top of the canopy. As for bark thickness, we compared species using the height allometric coefficients estimated using regression functions fit to raw data. For specific leaf area and wood density (stem specific density) we used data collected in the field following established measurement protocols (Pérez-Harguindeguy et al. 2013).

Maximum tree height tends to be correlated with several measures of plant size, including leaf size and seed size (Leishman et al. 1995, Díaz et al. 2016), and – among woody plants – is independent of the leaf economics spectrum as indicated by wood density and SLA (Díaz et al. 2016). For this reason, plant height has been proposed as a key axis of variation, particularly related to the ability to compete for light (Westoby 1998). However, savanna trees rarely compete for light (Archibald and Bond, 2003), and so, maximum tree height - as a functional trait - is less important within savannas. Instead, we were interested in the relative investment of resources, hence the use of allometric coefficients.

Trait Relationship Analyses

To assess associations among traits, we performed a Principal Components Analysis (PCA) on the standardized trait values. We performed this analysis on all species for which we had data for the four traits. To account for possible phylogenetic effects (nonindependence) we

performed a Phylogenetic Principal Components Analysis (Revell, 2009) using the phytools package in R (see Extended Data Figure S6.1). Phylogenetic relationships were reconstructed based on the species-level megaphylogeny of vascular plants in Zanne et al. (2014). From the 485 species present in our species pools, 299 matched directly to those sampled by Zanne et al. (2014). We added 100 species to genera using the same approach implemented in Phylomatic (Webb & Donoghue 2005) as in Qian & Jin, "scenario 3" (2016). Branch length are based on time (phylogeny in Zanne et al. 2014 calibrated using 39 fossils). The Phylogenetic Principal Components Analysis showed negligible differences to the PCA and was disregarded (see Extended Data Figure S6.1).

Continent and Biome classifications

We defined an a priori biome/vegetation classification of each species based predominantly on the classification of the data contributors. Where no such information was provided, we searched the literature and floras for vegetation descriptions, and looked at GBIF distribution records in conjunction with vegetation maps and tree cover maps. Any species which we were not confident classifying as savanna or forest, based on the above methods, were included as “unclassified”. A number of species were assigned a “Dry Forest” classification by data contributors. When this was the case we assigned them as “unclassified”. The definition of dry forests differs globally and no coherent or convincing definition has been proposed. This is partly due to difficulties in identifying this vegetation type from remote sensing, structural differences (Pennington *et al*, 2018; Dexter *et al*, 2018). Also, the term ‘dry forest’ is sometimes used, erroneously, to describe savannas, particularly those with high tree cover. We split species into three continents (South America, Africa, and Australasia) based on the sampling location, instead of the full distribution range.

Trait – Environment Relationships

Mean Annual Precipitation (MAP) and rainfall seasonality were calculated using the Tropical Rainfall Measuring Mission (TRMM) from 1998 to 2015 at 0.25 degree resolution. Tree cover (TC) data were derived from Hansen et al (2003), and used to classify the habitat type of each Quarter Degree Square (QDS), using a threshold of 65% tree cover, as Open (<65%) or Closed (>65%) habitats. Fire occurrences were based on a raster product used in Staver et al (in press) which used the MODIS Active Fires Product at a 1km scale.

To identify biome specific responses to environmental variables we applied a K-means partition (Legendre and Legendre, 1998), with the number of clusters defined by the partition yielding the highest Calinski-Harabasz value; two (see Extended Data Figure S6.3). We then compared the GBIF distribution records of the species within each cluster with environmental variables (fire and tree cover, see Extended Data Figure S6.3). Species level means were calculated for each environmental variable (Fire, TC, MAP) and the relationships between species level trait means, within each cluster, and environmental variables were analysed using parametric linear models, using appropriate data transformations (Figure 6.4). Using species occurrence records from the Global Biodiversity Information Facility (GBIF; http://gbif.org) we calculated an abundance weighted trait mean, for each cluster within each quarter degree grid square with three or more occurrence records, for bark thickness and height allometries. We then calculated a mean value for each QDS for a set of environmental variables. We restricted our analysis to elevations below 2000m a.s.l. to account for inconsistencies in the MODIS VCF dataset at high elevations.

We performed a generalized additive model (GAM) to predict height and bark allometries for each QDS across the tropics. The predictors chosen for the model were the biome, hemisphere/continent, and mean annual precipitation. We did not include fire as it covaried with MAP and TC. GAMs do not require a priori predictions of one parametric form or another (Crawley, 2007). This, in conjunction with the selection of variables based on expert knowledge, and not a stepwise selection process, avoids over-fitting of models. We built the models in R with the mgcv package (Wood, 2001).

6.3. Results and Discussion

When considering a wider range of biomes, such as flammable, open ecosystems versus fire-resistant, closed ecosystems, the oft-cited trade-off between dense wood and leaves, on the one end, and light wood and leaves, on the other, is less important than other axes of variation between different vegetation types. Principal components analysis revealed that axes orthogonal to this trade-off best differentiated savanna trees from wet forest trees (PC1; Figure 6.2a). The first of these axes, separating savanna trees from wet forest trees and explaining 43.3% of trait variance, was correlated with bark thickness and tree height allometric constants, which were themselves negatively correlated (see Figure 6.2b. $r = -0.6$, $N = 630$, $p < 0.001$). Interestingly, the relationship between height and bark thickness in forest tree species is highly significant ($r = -0.28$, $N = 362$, $p < 0.001$), whereas this is not the case in savanna trees ($r = -0.17$, $N = 154$, $p = 0.04$). In savanna systems, fire adaptations are certainly evident in the characteristically thick bark of savanna trees (Figure 6.3a) - thick bark is directly associated with trees surviving fires in savannas (Gignoux *et al*, 1997; Hoffmann et al. 2003; Charles-Dominique et al. 2017), where fires are frequent and relatively mild (Archibald et al. 2013) - while forest trees grew taller than savanna trees (see Figure 6.3b). This is consistent across continents (Extended Data Figure S6.2).

The second axis of the PCA (see Figure 6.2a) explained 27.1% of trait variance and correlated with both wood density and SLA. The trade-off between dense wood and thick leaves, on the one end, and light wood and thin leaves, on the other, is well known, and appears universal (Wright et al, 2004; Diaz et al, 2004; Chave et al, 2009; Reich, 2014). Extensive work has shown that the former (dense wood and thick leaves) is strongly associated with longevity, while the latter (light wood and large, thin leaves) is associated with rapid resource assimilation and growth (Diaz et al, 2004; Sterck et al, 2006; Wright et al, 2010; Reich, 2014). Wood density and SLA were negatively correlated across all species ($r = -0.16$, $N = 620$, $p < 0.001$), and within wet forest species ($r = -0.2$, $N = 390$, $p < 0.001$), but showed no significant relationship within savanna species ($r = -0.13$, $N = 116$, $p = 0.16$). Savanna trees, on average, had thick, heavy leaves (Figure 6.3c), similar to “slow” wet forest trees, and dense wood (Figure 6.3d), although mean wood density was similar across vegetation types.

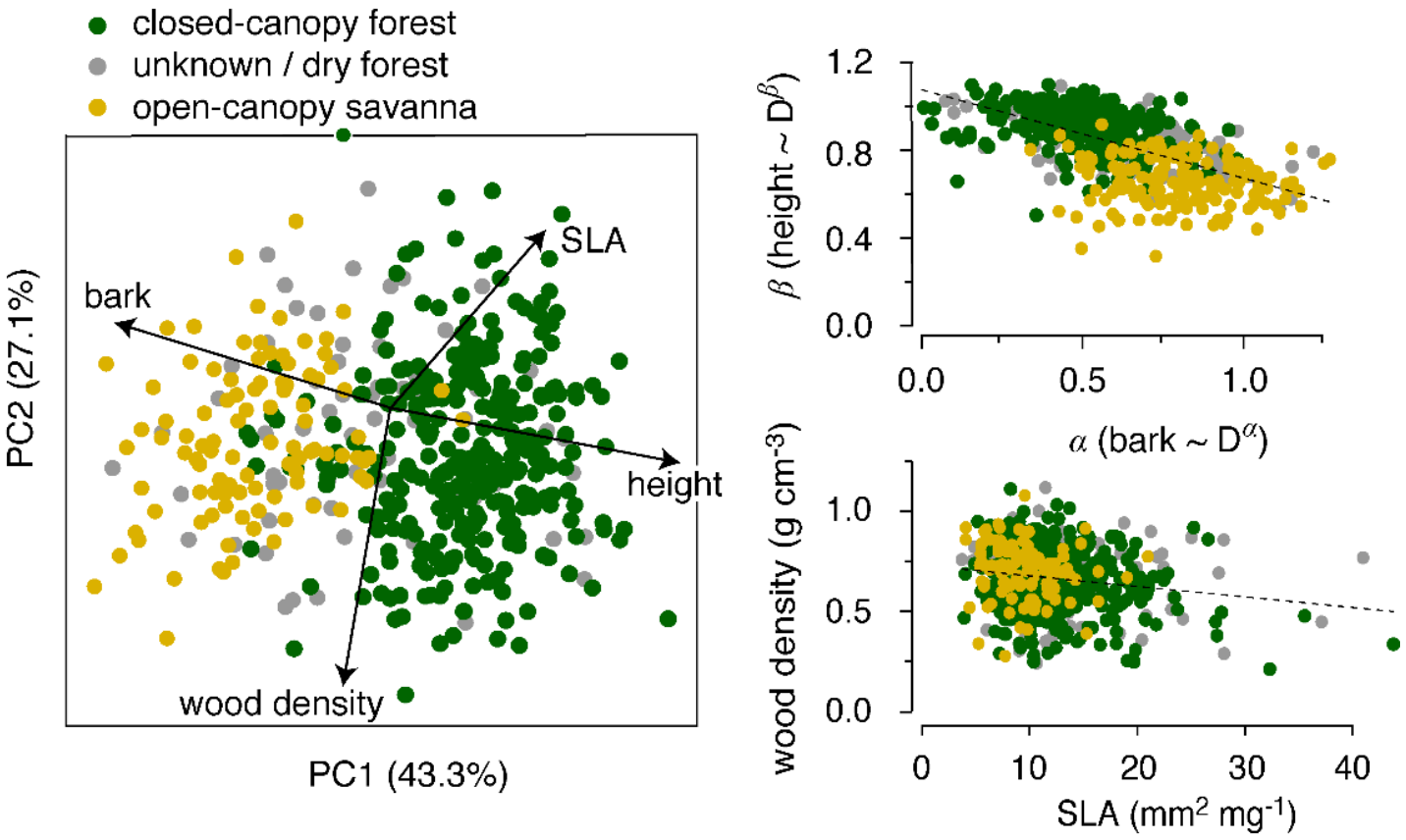


Figure 6.2. Principal components analysis of savanna (Yellow), wet forest (Green), and unclassified (Grey) species functional traits. Arrows indicate direction and weighting of vectors representing the four traits considered. Scatterplots on the right show trait interactions between species for bark thickness allometric coefficient versus height allometric coefficient, and Specific Leaf Area versus Wood Density. Data are scaled, points are species. Linear regressions (dashed lines) are fitted to all species.

Our sample of savanna trees were characterized by dense wood and thick leaves (Figure 6.3), and therefore fell out as species expected to be long-lived but relatively slow growing. This is consistent with some direct observational work; some savanna trees are known to persist for a few decades and sometimes grow very slowly (Prins & van der Jeugd, 1993; February et al, 2006; Staver et al, 2011). Moreover, dense wood is often associated with drought resistance (Hacke et al, 2001), an association that is found within the "Open" vegetation cluster (Figure 6.4). Since some (if not all) savannas have tree cover that is limited by water availability, drought adaptations may play a significant role in allowing trees to persist and thrive in savannas (Schenk et al. 2008).

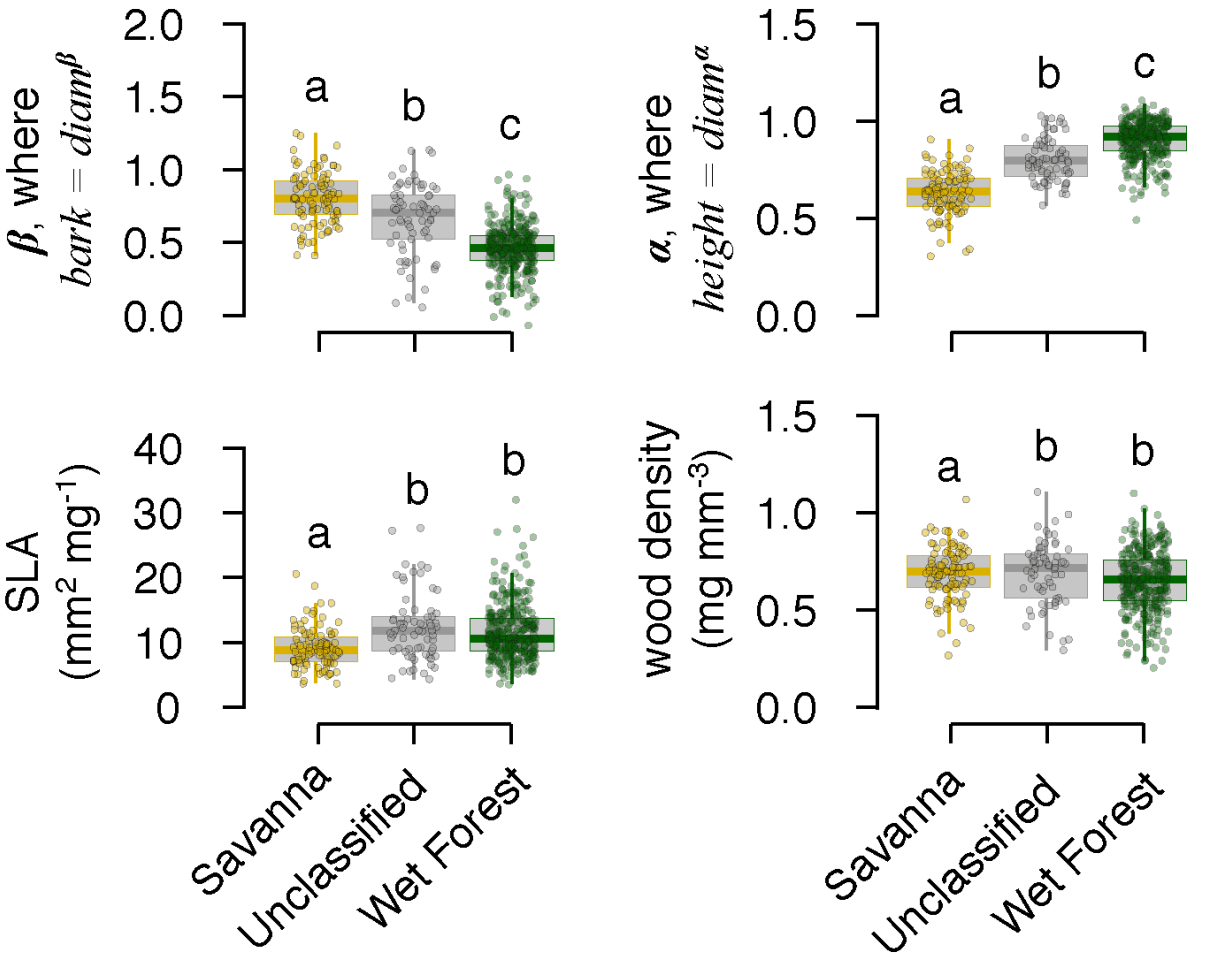


Figure 6.3. Bark Thickness (β) and Height (α) allometric coefficients, Specific Leaf Area and Wood Density of species found in savanna, wet forest and those that were not classified. Significant differences among species groups are denoted with asterisks. Whiskers show the maximum and minimum values, excluding outliers.

Slow growth and longevity, however, presents something of a paradox. Savanna trees have distinct demographic bottlenecks, each with a specific suite of strategies and adaptations. Savanna trees experience filtering processes that are constrained to certain demographic stages; saplings may be kept in a small, non-reproductive state for an extended period – a demographic bottleneck known as the fire trap – through repeated topkill by frequent fires (Higgins et al, 2000; Staver et al, 2009; Bond et al, 2012). Saplings escape the fire trap by growing tall enough that their buds are out of reach of the flame zone or by growing bark thick enough to protect their stems and buds (Gignoux et al, 1997; Clarke et al, 2013; Dantas and Pausas, 2013). Most work in savannas assumes that savanna trees must grow tall quickly (high sapling growth rates), in order to escape fire and herbivore effects (Trollope & Tainton, 1986; Higgins et al, 2000; Hoffmann et al, 2009; Staver & Bond, 2014). However, savanna trees

had wood and leaf traits usually associated with slow growth; savanna trees' dense wood and thick leaves indicate a life history geared towards survival, not rapid growth.

Theoretical work has argued, convincingly, that trees and grass coexist in savanna via the storage effect; frequent fires promote grass dominance, but large trees are long-lived and can persist until ecologically rare conditions allow a new cohort of trees to establish (Warner & Chesson, 1985; Higgins et al, 2000). Perhaps only tree species that are very long lived as adults (i.e. those with dense wood and thick leaves) can persist in grass-dominated ecosystems in the long-term. Here again, direct evaluation of whether limits to sapling-to-tree recruitment (Hanan et al, 2008; Prior et al, 2010) or to tree longevity actually limit tree persistence in savanna is warranted. The issue is not purely academic; for instance, savanna managers in Africa worry that elephants are killing large trees in savannas at unprecedented rates (Asner et al, 2009), with major potential impacts on savanna ecosystem structure.

If wood density positively impacts either sapling root or adult tree longevity, savanna woody species may nonetheless have allocation strategies that mitigate the expense of repeatedly producing high wood density shoots. Fire-adapted saplings are relatively sparsely branched, especially compared to saplings in less fire-prone savannas (Archibald & Bond 2003; Staver et al, 2012). Fire-adapted saplings also increasingly store carbon below ground in environments where fire is more frequent (Bhattachan et al, 2012; Tomlinson et al. 2012). We do not know whether savanna trees can modify their carbon allocation as they grow, but empirical evaluations have suggested that coarse root accumulation with sapling age appears to represent an ever-increasing respiratory cost, and not a growing source of non-structural carbon reserves (Schutz et al, 2009).

Despite recent advances in functional trait work, and a growing number of global syntheses, ecological generality (and related functional traits) has proven challenging. The 'holy grail' of traits based research is predictable ecological responses to environmental variables (Lavorel & Granier, 2002), however the focus on temperate and tropical forest systems, where succession and competition are the dominant ecological processes, had led to a specific set of rules about the effects on fitness of certain traits. Here we show that these rules are not general, and that certain relationships are biome specific (Figure 6.4).

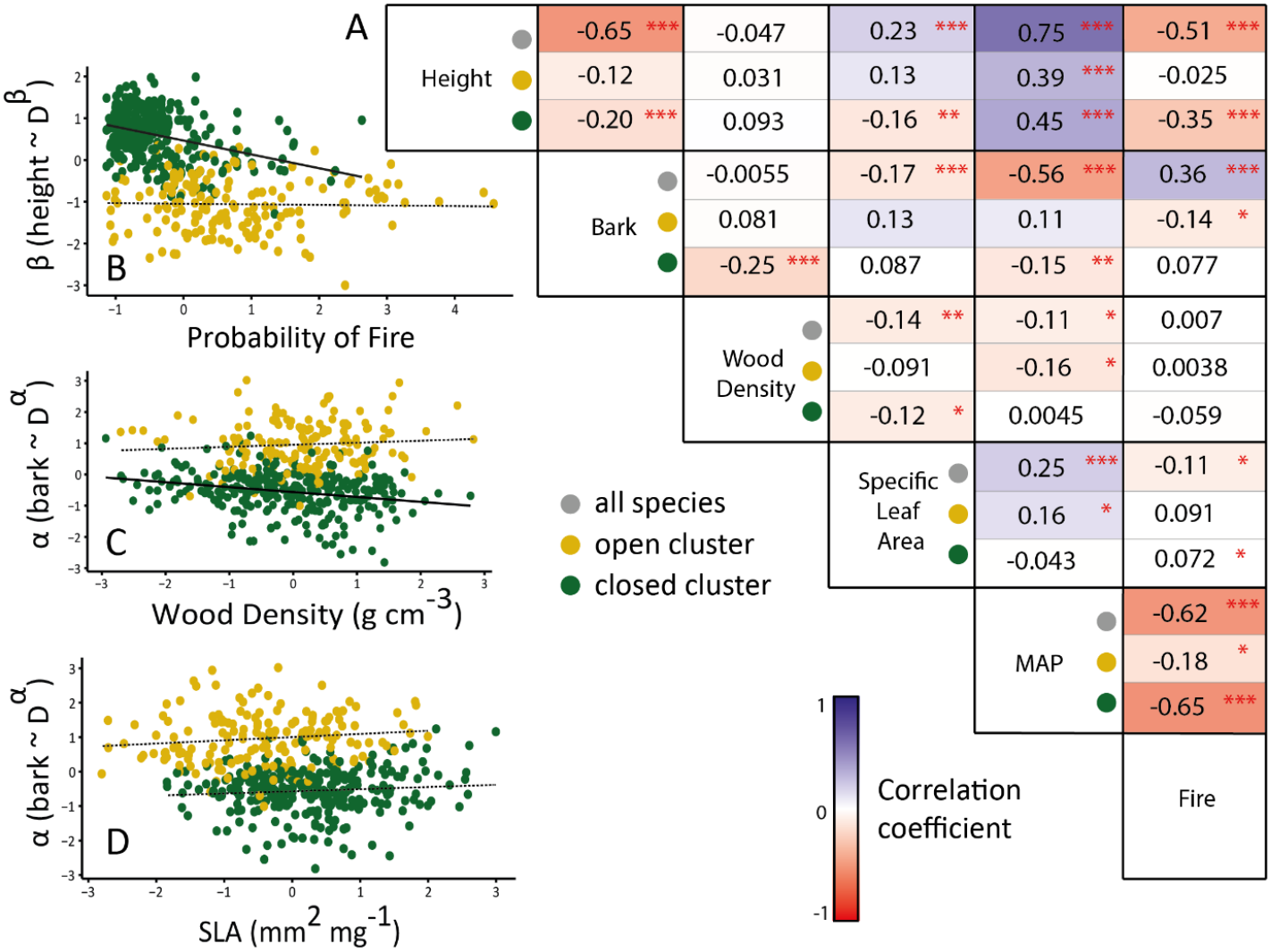


Figure 6.4. (A) Correlation matrix for trait-environment linear regressions for All Species (grey), and Open (yellow) and Closed (green) clusters. Red indicates a negative relationship, Blue indicates a positive relationship. Asterisks denote significant correlations. (B-D) Trait-environment relationships. Significant relationships denoted by solid lines.

The fire-light axis, orthogonal to the growth-mortality axes, separates out two vegetation clusters, identified by K-means clustering (Extended Data Figure S6.3). Species from both vegetation clusters occur within the climatic envelope suitable for alternative stable states, which possibly confounds the relationships between traits and environmental variables (Figure 6.4). There are however clear differences in the tree cover and probability of fire, between the two clusters (Extended Data Figure S6.3). It is vital that we identify traits that can be used in systems where disturbance is a regular occurrence.

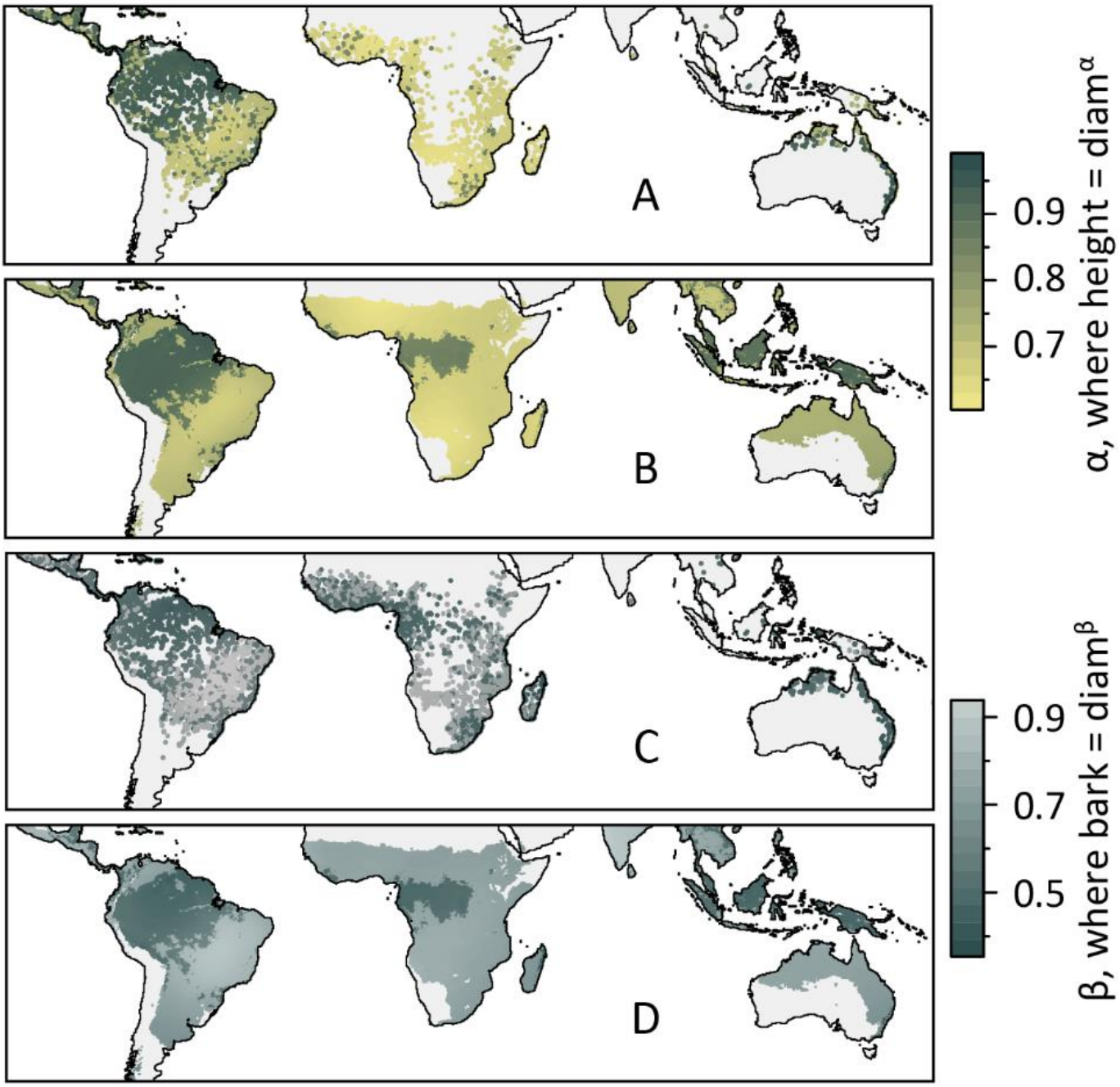


Figure 6.5. Observed (A & C) and predicted (B & D) height and bark thickness allometric coefficients.

Identifying and acknowledging the differences in plant traits between open and closed canopy systems, and a thorough understanding of their effects on fitness, is necessary to predict vegetation responses to global change, carbon storage and sequestration. A misclassification of the savanna biome, as low density tree cover of forest tree species, is harmful to both scientific enquiry and conservation efforts. Using the FAO definition of forests (>10% tree cover), Bastin et al (2017) identify "467 million hectares of forest that have never been

reported before" in dryland ecosystems. While this indicates a significant increase in the recognition of the importance of trees in savanna ecosystems contributing to global carbon storage, it would be foolish to assume the same drivers of ecosystem functioning, tree mortality and carbon allocation for savanna trees. Recent work (Pellegrini et al, 2017; Staver et al, in press) shows that without a consideration of bark thickness (and inferred fire resistance) in these systems, predictions of fire driven biomass losses are exaggerated. Here, we present global maps of predicted height and bark thickness allometric coefficients (Figure 6.5), for use in future studies, as a first step towards improving understanding of the global distribution of disturbance versus competition driven functional traits.

6.4 Extended Data

Extended Data Table S6.1. Data contributors, traits measured (B = Bark thickness, H = height, D = diameter, SLA = Specific Leaf Area, LMA = Leaf Mass Area, WD = Wood density), and references to publications.

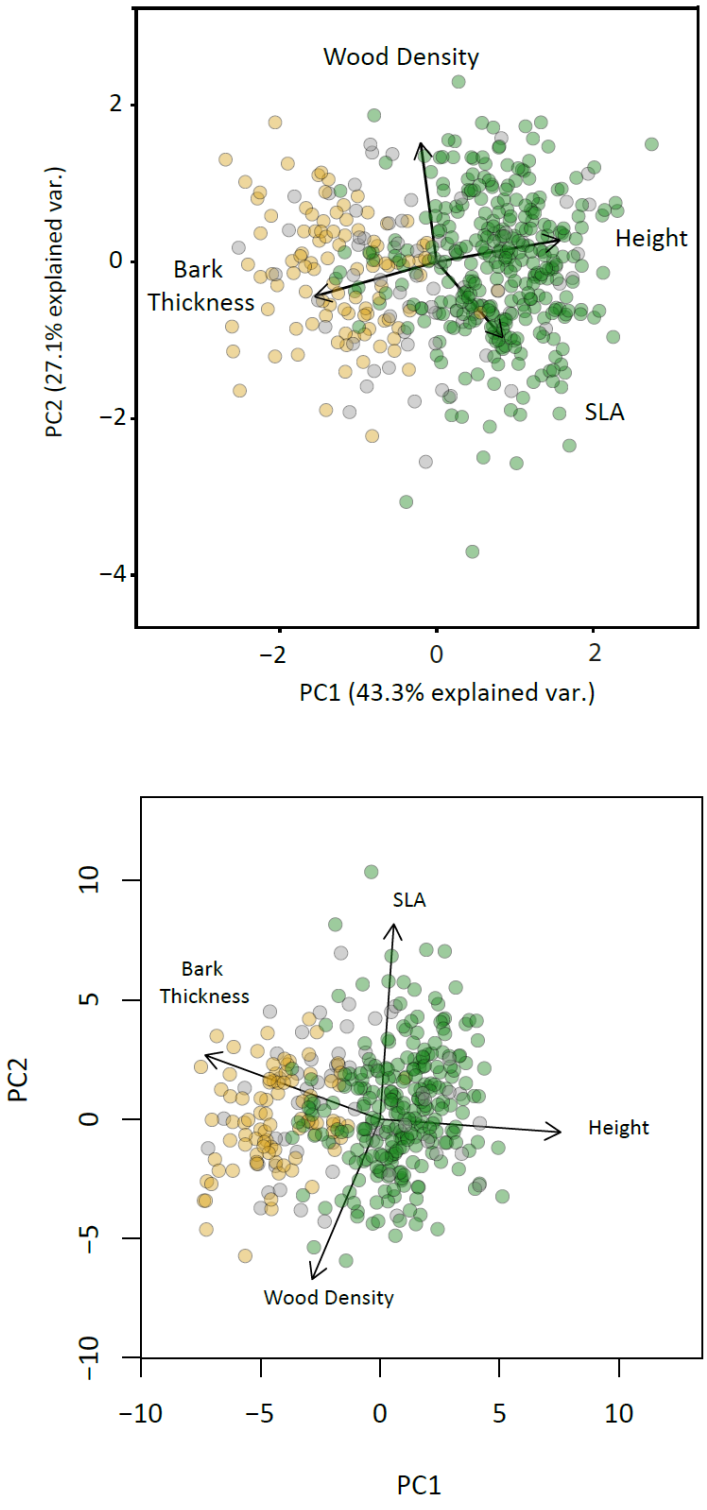
Name	No. of Species	No. of species used	Study Site	Traits	Reference to publication
Barlow	124	83	Amazon	B, D, H	Barlow, J. *et al.* (2012) *Bio Conserv* **154,** 1–8 (2012)
Bowers	30	30	Tanzania	B, D, H, LMA	*
Bond	15	15	Hluhluwe	B, D, H, SLA	South African Woody Plants Trait Database (ZLTP)
Geldenhuys	26	26	Western Cape	B, D, H	*
Ibanez	53	51	New Caledonia	B, D, H, SLA, WD	*
Gray	41	39	Brazil South Africa	B, D, H	*
Oliveras	17	78	Brazil	B, D, H, LMA	*
	73		Ghana	B, D, H, LMA	*
Fauset	224	46	Ghana	B, D	Fauset *et al* (2015) Nature Communications 6, 6857

*See note about publication details in the chapter preface

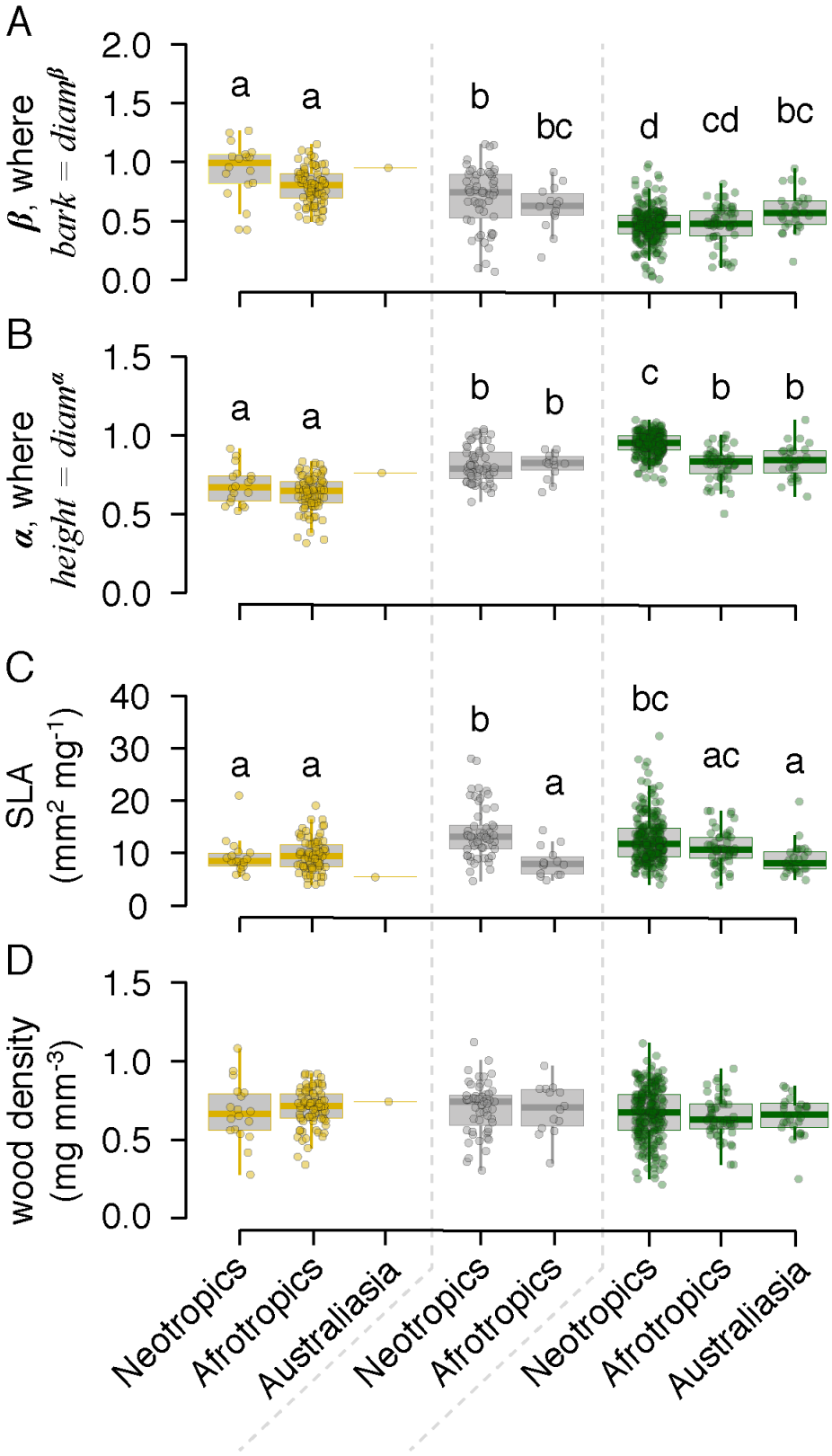
Extended Data Table S6.1 Continued. Data contributors, traits measured (B = Bark thickness, H = height, D = diameter, SLA = Specific Leaf Area, LMA = Leaf Mass Area, WD = Wood density), and references to publications.

Name	No. of species	No. of species used	Region	Traits	Reference to publication
Wigley	82	76	Afrotropics	B, D, H, SLA, WD	Wigley B.J. *et al* (2016) Journal of Ecology 104(5), 1357-1369.
Wolfe	27	24	Neotropics	B, D, H	Wolfe et al. (2014) Journal of Tropical Ecology 30, 133-142
Williams	6	6	Afrotropics	B, D, H	Williams et al. (2007) South African Journal of Botany 73,449-465
Syampungani	14	13	Afrotropics	B, D, H	*
Cardoso	19	15	Afrotropics	B, D, H, SLA	Unpublished PhD Thesis
Bridge		271	Various		*
Staver	200	200	Neotropics	B, D, H, SLA, WD	Staver et al, *in press*
This study	29	29	Afrotropics	B, D, H, SLA, WD	-

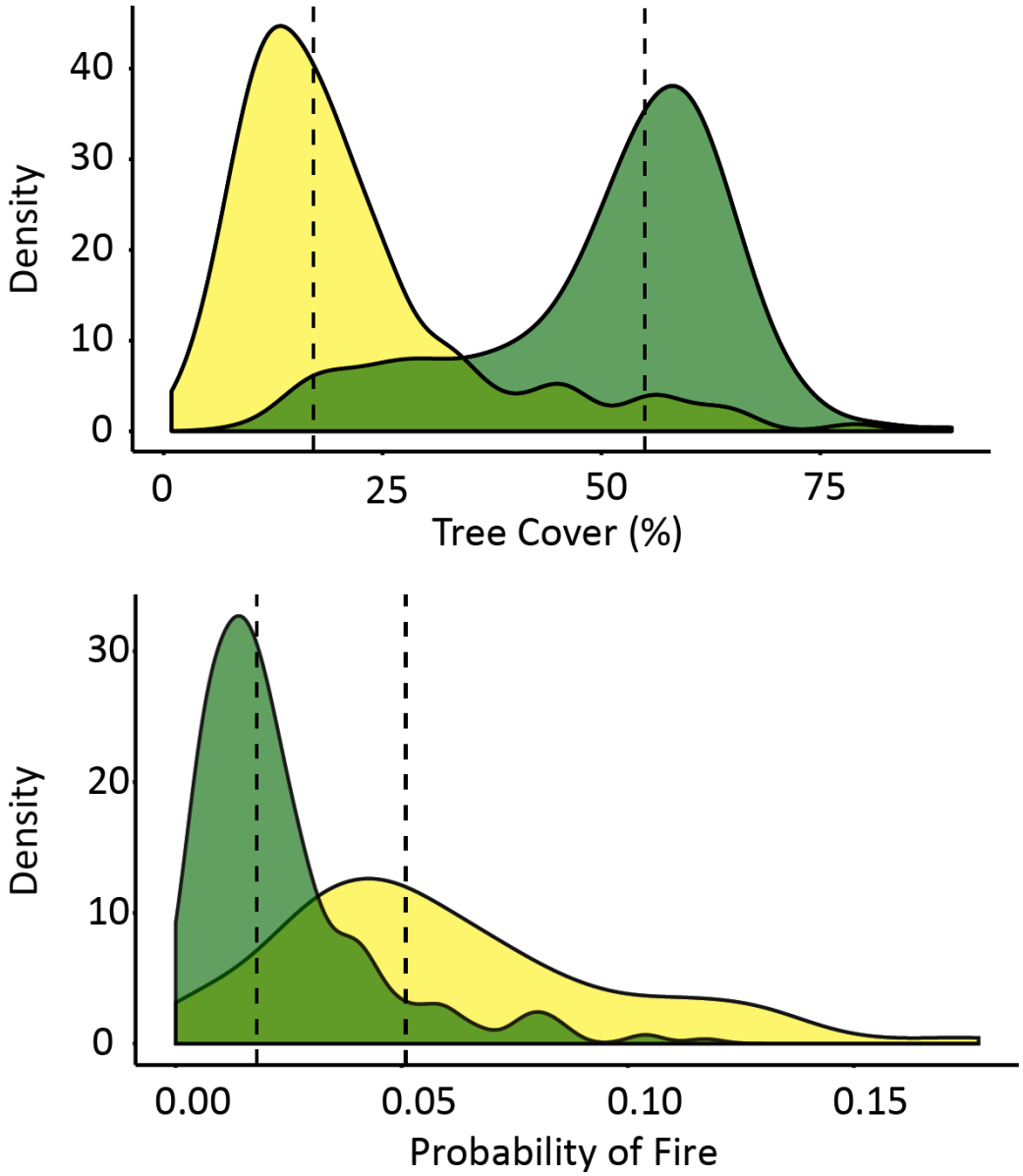
*See note about publication details in the chapter preface



Extended Data Figure S6.1. PCA vs Phylogenetic PCA showing minimal changes when phylogeny is controlled for.



Extended Data Figure S6.2. Bark Thickness (a) and Height (b) allometric coefficients, Specific Leaf Area (c) and Wood Density (d) of species found in savanna, wet forest and those that were not classified across three continents. Significant differences among species groups are denoted with asterisks. Error bars represent standard error.



Extended Data Figure S6.3. Tree Cover, from MODIS VCF data, and the probability of fire in a QDS, for the Open (yellow) and Closed (green) clusters.

Chapter 7

Synthesis

7.1. Summary of Key Findings

Recent decades have seen substantial increases in rates of deforestation in tropical forests, with areas of intact forest decreasing rapidly and fragmentation of forests reaching a critical tipping point (Watson et al, 2018; Taubert et al, 2018). Further fragmentation in forests can lead to a complete shift in vegetation and a loss of tropical forest biodiversity. The most commonly proposed solution to this is to plant more trees to restore fragmented landscapes, i.e. Bonn Challenge, REDD+. This is not however, always ecologically relevant and in some cases can be very harmful to the natural, biodiverse, open systems if they are misidentified as deforested areas requiring 'restoration' (Veldman et al. 2015; Bond 2016).

The designation of intact grassland as degraded forest suitable for restoration is often made in landscapes where the two co-occur, such as in tropical forest-grassy biome mosaics. At a landscape scale, such mosaics are caused by the interactions of fire and vegetation leading to interlocking patches of fire-adapted grassy biomes and the fire-sensitive forest biome (Manders, 1990; Bowman, 2000; Hoffmann et al, 2009) with abrupt boundaries between them (Jackson, 1968; Bowman, 2000; Warman and Moles, 2009). These mosaics are natural and not the result of deforestation. Contrary to much of the literature from the neotropics (e.g. Brando et al, 2014; Balch et al, 2008; Cochrane, 2003) fires from savannas usually go out on hitting forest margins in these mosaics. I, however, had the opportunity to study the rare occurrence of an extreme fire event that did cross the boundary, and so explore circumstances causing a catastrophic regime shift or recovery of a resilient forest boundary.

While the rarity of these extreme fire events makes this study interesting enough on its own, the location, Hluhluwe iMfolozi Park, is the ideal setting too. It is one of the oldest conservation parks in Africa. The forest-savanna mosaic occurs in the presence of the full suite of African megafauna, including elephants since the early 1980s (Owen-Smith *et al*, 2017). Frequent fires, the majority of which are ignited by park staff, occur in the park with occasional lightning ignitions and incursions of fires from neighbouring areas (Balfour and Howison, 2001). Rainfall is relatively high supporting frequent fires and true forests, not only thickets. Topography is undulating so fires vary in rates of spread depending on slope. Soils in the study area are very similar in their morphology and texture and geological substrate in forests and adjacent grassy areas (Gray and Bond, 2015). Also catenas, a typical feature of the

ancient African peneplains, do not exist, instead soils are strongly related to geological substrate. Thus HiP is at one end of a possible continuum in tropical systems in having a forest-savanna mosaic occurring across similar soils and substrates. Furthermore isotope analysis shows that forests were once savannas (West et al, 2001; Gray and Bond 2015; Gillson, 2015), centuries to millennia ago, thus savanna soils were invaded by forest.

In order to explore catastrophic regime shifts and recovery in forest-savanna mosaics, I initially set out to determine the drivers of vegetation distributions and dynamics. In Chapter 3 I explored correlates of forest distribution and whether or not forests remained static over time. In Chapter 4 I tested the idea that fire is the major determinant of the location of the two mosaic elements, based on the oldest historical imagery available to capture patterns least impacted by land use changes, road development and settlements. Results from these chapters show vegetation distributions have not remained static over time, the boundaries between vegetation types have shifted substantially. These changes in vegetation are not homogeneous, either temporally (rates and directionality of change differ between time periods) or spatially (fire refugia and patch size influence persistence, expansion and contraction processes) throughout the study. Simulated fire behaviour patterns are good predictors of fire-sensitive vegetation distributions, as long as the fire weather data are based on the 'natural' fire season.

At a landscape scale, it is difficult to explain forest-savanna mosaic patterns by bottom-up drivers. The idea is deeply entrenched and supporters do not take kindly to the suggestion of alternative explanations (Lloyd and Veenendaal, 2016). However, there are few testable hypotheses for how these patterns develop. In HiP there are only minor differences in soil fertility between forest and grassy systems (Gray and Bond, 2013). Rainfall at a broad scale is a good predictor of forest - there are no forests where there is too little rainfall no matter the predicted fire behaviour - it does however not explain boundaries on the ground. It is important to note the effect of scale of observation on the understanding of drivers. Scale is a fundamental concept in ecology; Levin (1992) describes it as "the central problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology". Patterns and processes observed are frequently scale-dependent; the scale of observation may determine the importance or effect of certain factors (Luoto and Hjort, 2006; Sandel and Smith, 2009). A simple landscape scale model of fire behaviour, which

incorporates the effects of rainfall, provides a clear picture of the association between fire refugia and historical forest extent and boundaries.

After identifying the drivers of vegetation distribution and dynamics, the next important step was to understand how these changes occur. Sufficient rainfall allows for the possibility of forests in the landscape. The locations where this possibility are highest are within fire refugia. At a finer temporal and spatial scale, the on-the-ground location of the boundary between vegetation types is driven by previous fires and the response of vegetation to those fires. Understanding events at the boundary between biome states is important for the future of forests and savannas. In Chapter 5 I present evidence from the field of how fires can open up forests allowing the spread of savannas. It does not require logging to change fuel properties. However, it is hard to do and takes exceptional fires. Both thicket and forest patches were burnt in the Hluhluwe-iMfolozi Game Reserve in a 'firestorm', an extreme fire event driven by high winds and dry, hot conditions.

Hoffmann et al (2012) proposed two critical thresholds that govern the success of trees in a fire prone environment; the 'fire-resistance threshold' and the 'fire-suppression threshold'. The 'fire-resistance threshold' is reached when individual trees have accumulated sufficient bark to avoid stem death, whereas the 'fire-suppression threshold' is reached when an ecosystem has sufficient canopy cover to suppress fire by excluding grasses (Hoffmann et al, 2012a). There were major differences in my system from the model proposed by Hoffmann et al (2012) in tree life histories. I identified two separate post-burn recovery pathways. Firstly, within thickets, the majority of existing trees which experienced topkill in the 2008 firestorm were able to resprout basally. The growth rate of these resprouts is higher than that of seedlings due to existing underground storage. The rate at which these resprouts grow is vital for reaching the 'fire-suppression threshold'. Once the ecosystem has a sufficient fire free interval to allow canopy closure, the flammable grassy layer is shaded out and the system returns to its original state. This did not happen in Hluhluwe. After the fire storm, the interval to the next fire was not long enough to allow canopy closure in the thickets, which have since been colonised with savanna tree species and grasses and have burnt again.

The second pathway is exclusive to forests. Tree mortality following fires is much greater in forests than in savannas, despite similarities in the bark thickness of tree trunks in some tree species. Forest trees do not seem to reach the 'fire-resistance threshold' proposed by

Hoffmann et al (2012). Instead the emphasis is placed on reaching the 'fire-suppression threshold' where canopy shading excludes flammable grasses. Following a fire, forests recovered from a seed bank. There is, however, a successional pathway where rapid growing pioneer forest species establish from seedbanks and generate a microclimate/environment suitable for later-successional forest species to establish. Post-logging fires in the neotropics are usually low intensity but very damaging. Unlike studies of burning in these logged forests of the neotropics, and the Amazon, the forests at HiP have natural boundaries with savannas and frequent savanna fires are the norm. 'Savannization' in the Amazon is typically studied in extensive patches of forest which have been logged, or where grasses have been planted by ranchers, so that the trees are likely to be completely 'naïve' to fire (Balch *et al*, 2015). In HiP, forest patches naturally abut savannas, the system has its native herbivores, and human impacts are low. Forest margins appear to be far more resilient, where they occur in mosaics with savannas in Africa, than forest interiors in the neotropics.

A large portion of the terrestrial landmass is covered by disturbance-prone vegetation. Functional trait studies have focused primarily on competition for resources, not on understanding key differences between biomes, such as differing responses to disturbance. If forests and savannas are ASS then they should persist long enough for discrete traits to diverge in the two systems with contrasting fire responses at the center of these trait differences. In Chapter 6 I present a global analysis of many tree species supporting this finding. Savannas are not simply areas with less trees than forests, there are distinct savanna growth forms that respond differently to drivers (Hoffmann *et al*, 2005; Gotsch *et al*, 2010). Allometric relationships and carbon allocation strategies differ between biomes and to fully understand and model global carbon budgets it is vital we understand these differences.

In the last few years the functional trait literature on disturbance-prone ecosystems has taken off (Clarke *et* al, 2013; Fidelis *et al*, 2014; Pausas *et al,* 2018), with a wider acceptance of the role of disturbance regime, as opposed to climate, determining the distribution of savanna trees (Stevens *et al*, 2018). Wigley *et al* (2016) demonstrate weak relationships between commonly measured traits and environmental gradients in savanna trees across Southern Africa, which corroborates the results in Chapter 6. The traits governing fitness of savanna trees differ between demographic stages and the disturbance regime (type, history, severity, intensity of disturbance). Disturbance prone trees have developed a number of strategies,

including clonal spread and belowground bud banks allowing basal resprouting (Fidelis *et al*, 2014; Pausas et al, 2018), insulated buds which are protected from fires and allow for epicormic canopy resprouting (Burrows, 2013; Charles-Dominique *et al*, 2015), to cage-like structures and spinescence (Charles-Dominique *et* al, 2016) to protect from herbivores.

The difficulty going forward is to assimilate these traits into existing global frameworks. Much of the earlier trait based literature was assembled in temperate deciduous forests (Grime, 1974) and later in tropical forests where net primary productivity (NPP) was originally thought to be related to biomass (Whittaker, 1975). Subsequent studies showed productivity asymptotes and even declines when biomass is high (Keeling and Philips, 2007) Despite lower biomass, net primary productivity in savanna and grassland ecosystems is on par with that of forest ecosystems (Oliveras *et al*, 2014). Biodiversity and ecosystem services of these systems are heavily influenced by ecosystem structure which is why it is vital for 'global' trait syntheses, which rely heavily on climate driven processes and responses and pay little to no attention to consumer-related traits (e.g. Diaz *et al*, 2016), to acknowledge this.

7.2. Where to from here?

Despite my dismissal of the importance of bottom-up drivers throughout my thesis, I do think there are situations where soil characteristics do play a role in determining savanna-forest boundaries. Areas such as HiP are however, on the other end of the continuum where the role of bottom-up drivers are minimal. We need to investigate spatial patterns in mosaics under a wider range of conditions in order to integrate bottom up and top down approaches. I believe these seemingly incongruent theories can be unified into a hierarchy of drivers if we identify the spatial and temporal scale of drivers.

Fire seasons seem to be increasing in length globally (Jolly *et al*, 2015). What does this mean for the future of extreme fires? Fire intensity peaks after the peak in burnt area and highest number of fires, typically (in HiP at least) at the change of the seasons (Archibald et al, 2010). Does atmospheric stability have a role to play in the ability for a fire to develop its own weather? If so, can we detect and model when this is most likely to occur? Firestorms all seem to have one thing in common, a well-developed convection column. This allows the fire to create its own weather (i.e. it is effected by intrinsic rather than extrinsic weather conditions).

A potential area for the future research of extreme fires should focus on the synoptic conditions that trigger firestorms. Recognizing the weather systems that lead to prolonged periods of high wind speeds, low humidity and high temperatures may allow for an advanced warning of firestorms ahead of standard Fire Danger Indices.

There is still much to be understood about forest 'pioneers' and fire resilient margins. By identifying natural mosaics, with 'non-naïve' boundaries, and exploring the differences between forest edge species and those in the interior we will advance our understanding of boundary dynamics in forest-savanna mosaics. These edge species might be expected to have a long history of exposure to savanna fires. Fire suppression within these mosaics may lead to a loss of resilience of forest margins as the seed bank of these pioneer species is depleted over time. In the future, chance fires which are not suppressed will lead to larger losses of forest area as shade intolerant pioneer species are not readily available to reclaim forest edges.

Bush encroachment is widespread and became a major concern by end of 20th and beginning of 21st century, with far reaching consequences for biodiversity and ecosystem services (Eldridge et al., 2011; Smit and Prins, 2015; Stanton Jr et al., 2018). Species assemblages of birds, arthropods and mammals undergo a switch in composition and functional type with changes in woody cover (Blaum et al., 2009; Leitner et al., 2018; Péron and Altwegg, 2015; Stanton Jr et al., 2018, Parr *et al,* 2012). Bush encroachment affects access to grazing through a loss of grass biomass and ultimately a decrease in rangeland productivity. Conversely, more woody biomass provides services such as materials for fuel and building (Archer *et al*, 2017). Understanding the nature and extent of these impacts in African savannas is crucial due to the direct dependence of a large marginalized, vulnerable, rural population on savanna ecosystem services for agriculture and grazing.

How does one reconcile lengthening fire seasons and more extreme fires with an increase in woody biomass? And what predictions can we make for the future of African savannas and forests? These processes are all influenced by vegetation traits, producing vastly different patterns in similar landscapes (Osborne et al, 2018). As climate changes, there is the potential for surprises such as more firestorms, as fire regimes are closely coupled to climate. An increase in these extreme events would allow more opportunities for catastrophic regime

shifts and losses of forest vegetation. This, as shown in Chapter 5, is dependent on the colonisation by flammable fuels and regular subsequent fires. It is important then to consider how increasing atmospheric CO_2 concentrations affects the productivity of these system. Increasing atmospheric CO_2 will positively affect woody plant growth rates and resprouting rates following disturbances like frost, fire and herbivory (Bond & Midgley 2000; Hoffmann et al. 2000; Kgope et al. 2010), and increase plant water use efficiency (Polley et al. 1997; Morgan et al. 2004; Donohue et al. 2013), allowing for more rapid canopy closure following firestorms. Regime shifts might be less expected in areas of low productivity as seedling survival rates and tree growth rates increase. In areas of high productivity, fuel production is not a limiting factor, frequent high intensity fires are however often prohibited by wet fuels (Archibald *et al*, 2013), leading to questions about the future of rainfall variability and prolonged periods of extreme fire weather conditions. We need answers to the questions of how one reconciles lengthening fire seasons and more extreme fires with an increase in woody biomass to accurately predict the future of African savannas and forests.

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